Conservation assessment of Scarabaeine

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in South Africa, Botswana and Namibia:
IUCN Red List categories,
atlas and ecological notes

Adrian L.V. Davis, Christian M. Deschodt & Clarke H. Scholtz

SURICATA 6

Photograph: Marinda Koekemoer

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by:
Adrian L.V. Davis
Christian M. Deschodt
&
Clarke H. Scholtz

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South African National Biodiversity Institute

Pretoria
2020

SURICATA

Suricata is the genus name of the suricate (*meerkat*), which is near-endemic to the arid western parts of southern Africa (occurring in Namibia, South Africa, Botswana; and just entering into a small area in the extreme south of Angola). Behaviourally, suricates are socially inclusive and innately inquisitive, symbolising the commitment of the South African National Biodiversity Institute (SANBI) to include all biodiversity and serve all of Africa, and the scientific curiosity that precedes and drives research and publication of research results. Sister journal to SANBI's *Strelitzia*, *Suricata* is a peer-reviewed journal and publishes original research such as monographs, revisions, checklists, Red Lists, Atlases and Faunas of any taxa belonging to Regnum Animalia (the Animal Kingdom).

By Adrian L.V. Davis, Christian M. Deschodt & Clarke H. Scholtz

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Preamble

Around three years elapsed between completion (November 2017), review and publication of the book. As taxonomic revision is an ongoing process, a number of new tribes, genera, species and synonymies were described over those three years. For the most part, accounts for these new taxa were not included in the book as extensive changes would have been required to sections that summarise the composition and distribution of the southern African dung beetle fauna. However, the new taxa and changes in status are listed below together with citations to the publications in which they were described (see **References**).

New tribes

1. Some of the clades defined as 'Basal Scarabaeinae' within the most recent global phylogeny for the subfamily Scarabaeinae (Tarasov & Dimitrov 2016) have subsequently been described as new tribes (Davis et al. 2019) although, here, they remain listed within the tribe Canthonini (by common usage) or Deltochilini (by precedence) pending a full revision of tribal classification; see, also, introduction to the tribe Canthonini: Clades 1A, 1B, 1C, as well as notes in accounts for affected genera.

   1A: Tribe Odontolomini Davis, Deschodt & Scholtz, 2019 (one genus: centred in southern Africa).

   1B: Tribe Byrrhidiini Davis, Deschodt & Scholtz, 2019 (seven arid SW African genera: South Africa, Namibia).

   1C: Tribe Endroedyolini Davis, Deschodt & Scholtz, 2019 (seven SE African forest genera: South Africa).

2. See recent revisions of tribal, generic and subgeneric composition (Tarasov & Dimitrov 2016; Daniel et al. 2020) updated in the introductions to the genus *Epirinus* Dejean, 1833, and the tribe, Sisyphini Mulsant, 1842; also noted in generic and species accounts for the Sisyphini.

3. New tribe pending (Catharsiini Takano) for the genera, *Catharsius* Hope, 1838, and *Metacatharsius* Montreuil, 1998 (see Takano 2018, unpublished).

New genera, species and synonyms in southern Africa plus missed species

1. *Catharsius laticeps* Boheman, 1857: missed sand and dune forest species of NE KwaZulu-Natal and SE Mozambique coast (see notes in species account).
2. *Proagoderus gangloffi* Josso & Prévost, 2001: missed elephant dung specialist species of E Kaokoveld, N Namibia.
3. New genus in the tribe Onthophagini Burmeister, 1846 (Dierkens et al. 2017); *Jossonthophagus* Dierkens, Moretto & Génier, 2017, accommodates the species of *Onthophagus* Group 14; no species accounts for two species recorded in the target area of southern Africa.
4. New genus and species from arid SW Namibia (Deschodt & Davis 2018) in the new flightless tribe, Byrrhidiini Davis, Deschodt & Scholtz, 2019 (formerly incorporated into tribe, Canthonini).
   a. *Ausmontins* Deschodt & Davis, 2018, and *Ausmontins jacobsi* Deschodt & Davis, 2018, from near Aus.
   b. *Namakwanus kamfferi* Deschodt & Davis, 2018, from Bloedkoppe, Namib Desert.
   c. *Namakwanus minutus* Deschodt & Davis, 2018, from the Nubib Mountains.
   d. *Namaphilus nubibmontanus* Deschodt & Davis, 2018, from the Nubib Mountains.
   e. *Namaphilus tirasmontanus* Deschodt & Davis, 2018, from the Tiras Mountains.
5. New taxa in the *Garreta lugens* (Fairmaire, 1891) species group (Davis & Deschodt 2018).
   a. *Garreta namalugens* Davis & Deschodt, 2018, from the rocky W mountain escarpment of Namibia.
   b. See species account for *Garreta australugens* Davis & Deschodt, 2018, from SE Africa, recently separated from *Garreta lugens* (Fairmaire, 1891), from East Africa.
6. New species of the flightless genus, *Macroderes* Westwood, 1842, from SW South Africa (Abdalla et al. 2018); includes additional distribution records for previously described species.
   a. *Macroderes cederbergensis* Abdalla & Deschodt, 2018, from the Cederberg, SW Western Cape.
   b. *Macroderes gifboomi* Abdalla & Deschodt, 2018, from Gifberg near Vanrhynsdorp, SW Western Cape.
   c. *Macroderes leipoldti* Abdalla & Deschodt, 2018, from the Hantamsberg, SW Western Cape.
   d. *Macroderes oreatus* Abdalla & Deschodt, 2018, from Richtersveld National Park, Namaqualand.
   e. *Macroderes porselinus* Abdalla, 2018, from Porseleinberg, SW Western Cape.
   f. *Macroderes soleiana* Abdalla & Deschodt, 2018, from the Cederberg, SW Western Cape.
   g. *Macroderes tortuosus* Abdalla & Deschodt, 2018, from the Gifberg near Vanrhynsdorp, SW Western Cape.
   h. Validity confirmed for *Macroderes pristinus* Sharp 1880, from Diamondfields, Namaqualand.
7. New species of southern African *Sisyphus* Latreille, 1807 (Daniel et al. 2018).
   a. *Sisyphus swazi* Daniel & Davis, 2018, from forest in Eswatini (formerly Swaziland).
   b. *Sisyphus inconspicuus* Daniel & Davis, 2018, from shaded vegetation in SE Africa: South Africa, Mozambique.
   c. *Sisyphus australis* Daniel & Davis, 2018, from shaded vegetation on the south coast of South Africa.
8. Review of *Scarabaeolus* (Balthasar, 1965a), by Zídek and Pokorný (2018) including new southern African species with *Scarabaeolus* treated as a subgenus of *Scarabaeus* Linnaeus, 1758.
   a. *Scarabaeolus krugeri* (Zídek & Pokorný, 2018) from Kruger National Park, South Africa (=unpublished synonym of *Scarabaeolus planipennis* (Davis & Deschodt, 2015)).
   b. *Scarabaeolus lizleri* (Zídek & Pokorný, 2018), which separates NW South African material from the Namib Desert dune field species, *Scarabaeolus rubripennis* (Boheman, 1860); *S. lizleri* material included, here, in the species account for *S. rubripennis*.
   c. *Scarabaelous namibensis* (Zídek & Pokorný, 2018) from the central Namib Desert and Kaokoveld, Namibia (see species account).
   d. *Scarabaeolus fragilis* (Zídek & Pokorný, 2018) from Springbok, Namaqualand, South Africa.
   e. *Scarabaeolus rugosipennis* (Zídek & Pokorný, 2018) from Makgaberg Plateau, Limpopo, South Africa; needs to be re-examined as a probable synonym of *Scarabaeolus niemandi* (Deschodt & Davis, 2015).
   f. *Scarabaeolus cunene* (Zídek & Pokorný, 2018) possibly from E Hartmann dune field, N Namibia.
   g. *Scarabaeolus orientalis* (Zídek & Pokorný, 2018) from farm Rhenosterpoort, Gauteng, South Africa (=unpublished synonym of *Scarabaeus karae* Davis & Deschodt, 2017).

h. *Scarabaeolus similis* (Zídek & Pokorný, 2018) from Pienaars River, Gauteng, South Africa.
i. Again, incorrectly synonymises *Scarabaeolus reichei* (Waterhouse, 1890) with *Scarabaeolus canaliculatus* (Fairmaire, 1888); in this book, the two species are treated as valid, *S. canaliculatus* from the southern Namib Desert and *S. reichei* from the W Coast of South Africa.

9. Review of African *Garreta* Janssens, 1940a (Pokorný & Zídek 2018); notes of relevance to southern Africa:
   a. Overturns the Moretto and Génier (2015) revalidation of SE African *Garreta wahlbergi* Boheman, 1857, by synonymising it, once more, with widespread African species, *Garreta nitens* (Olivier, 1789).
   b. Cites *Garreta fastiditus* (Fahraeus, 1857) as a valid South African species although we consider its type locality suspect and provide no species account.
   c. Extends range of *Garreta caffer* (Fahraeus, 1857) across that occupied by subspecies *Garreta laetus olivaceus* (Quedenfeldt, 1883), which is synonymised with *Garreta laetus* (Hope, 1842).

10. New genus in the tribe, Onthophagini Burmeister, 1846 (Roggero et al. 2019); transfer of *Onthophagus* species to the new genus, *Tiaronthophagus* Roggero, Moretto, Palestrini & Barbero, 2019 (see notes under Group 24 in introduction to the genus, *Onthophagus* Latreille, 1802); species in South Africa and Botswana only:
    a. *Tiaronthophagus ebenus* (Péringuey, 1888) (see species account under *Onthophagus ebenus*).
    b. No species account for *Tiaronthophagus aequatus* (*Onthophagus aequatus* Péringuey, 1900) recorded in Botswana.

11. New species and synonyms of *Epirinus* Dejean, 1833, from South Africa and a new record from Namibia (Deschodt et al. 2019).
    a. *Epirinus inparrugosus* Deschodt & Davis, 2019, from Blesberg-W, Swartberg, Eastern Cape.
    b. *Epirinus jacobsae* Deschodt & Davis, 2019, from Mapelane, NE coastal KwaZulu-Natal.
    c. *Epirinus muellerae* Deschodt & Davis, 2019, from central Drakensberg and E central Lesotho.
    d. *Epirinus pseudorelictus* Deschodt & Davis, 2019, from coastal NE Eastern Cape.
    e. *Epirinus schoolmeestersi* Deschodt & Davis, 2019, from Baviaanskloofberg, Eastern Cape.
    f. See species accounts for *Epirinus hluhluwensis* Medina & Scholtz, 2005, and *Epirinus ngomae* Medina & Scholtz, 2005, which are retained even though they have, now, been synonymised with *Epirinus davisi* Scholtz & Howden, 1987, whose distribution records have been expanded to Eswatini.
    g. See species account for *Epirinus flagellatus* (Fabricius, 1775) for which a new distribution record expands the generic distibution to N Namibia (Okonjima Nature Reserve).

12. New species and a revalidation from synonymy in South African *Gyronotus* van Lansberge, 1874a (Deschodt & Davis 2019).
    a. *Gyronotus dracomontanus* Deschodt & Davis, 2019, from the central Drakensberg grasslands near Bergville.
    b. *Gyronotus ovalis* Deschodt & Davis, 2019, from grassland at the edge of Nkandla Forest, Zululand.
    c. *Gyronutus kearneyorum* Deschodt & Davis, 2019, from grassland on Mount Sheba, Mpumalanga.
    d. Revalidation of *Gyronotus marginatus* Péringuey, 1888, from coastal forest near East London, Eastern Cape, which is removed from synonymy with *Gyronotus pumilus* (Boheman, 1857), but remains included in the species account for that species in this book.

13. Subgenus *Hyalonthophagus* Palestrini & Giacone, 1988, formally raised to genus status with description of a new species (Deschodt et al. 2019).
    a. *Hyalonthophagus pulcher* Deschodt & Davis, 2019, from the Northern Cape, South Africa.

14. New species of *Versicorpus* Deschodt, Davis & Scholtz, 2011, from Namibia (Deschodt & Sole 2019).
    a. *Versicorpus daures* Deschodt, 2019, from Brandberg (mountain) in W central Namibia.

Exceptions

The taxonomic updates to current nomenclature effected during the review of this atlas (see above) are also noted in the generic and species accounts where applicable. However, in a few further species accounts, taxonomic treatment also diverges from the currently accepted nomenclature. These species are listed below.

1. *Euonthophagus vicarius* (Péringuey, 1901) is treated here as a valid species although it is currently still listed as a synonym of *Euonthophagus carbonarius* (Klug, 1855).

2. *Gymnopleurus pumilus* Reiche, 1850 is treated here as a tentatively valid species although it is currently still listed as a synonym of *Gymnopleurus virens* Erichson, 1843.

3. *Kheper vethi* (van Lansberge, 1886) is treated here as a species of *Kheper* Janssens, 1940b although it currently remains classified as *Scarabaeus vethi* van Lansberge, 1886.

4. *Onthophagus cretus* Péringuey, 1901 is treated here as a valid species although it is currently still listed as a synonym of a poorly known species, *Onthophagus setosus* Fahraeus, 1857.

5. *Onthophagus peringueyi* Shipp, 1895 is currently classified as a synonym of *Onthophagus suturalis* Péringuey, 1888, which we consider a synonym of *Onthophagus pallidipennis* Fahraeus, 1857 along with another currently valid species, *Onthophagus politissimus* d'Orbigny, 1908.

6. *Onthophagus venustulus* Erichson, 1843 is treated here as a valid species although it is currently still listed as a synonym of *Onthophagus variegatus* (Fabricius, 1798).

INTRODUCTION

A. IMPORTANCE OF GROUP

Scarabaeine dung beetles (Order: Coleoptera; Family: Scarabaeidae; Subfamily: Scarabaeinae) have received a great deal of attention in recent decades. Much of the attention stems from programmes to augment control of dung and dung-breeding flies in farm rangeland by introducing European and African dung beetle taxa into Australia, the Americas and, lately, New Zealand. Research on dung beetle ecology to assist selection of species for introduction has, subsequently, developed in several directions. Dung beetles have been widely used to bioassay non-target effects of livestock pesticides in farm rangeland. They have also been widely used as biological indicators in ecological impact assessments (EIA) and studies of farm health, as well as in conservation studies investigating the effects of habitat modification, habitat fragmentation and loss of mammals producing preferred dung types. Therefore, an atlas of the dung beetle species found in South Africa, Botswana and Namibia, is long overdue. This atlas provides photographs of over 540 species together with notes on their taxonomy, distribution, ecology and conservation status. As the alpha taxonomy is incomplete, the atlas is also incomplete, although it does comprise accounts for most species in eight out of nine tribes of dung beetles found in the target region (Onthophagini excepted). Although numbers of species and genera are quoted for the nine tribes, it should be noted that these are frequently changing due to revisions of pre-existing nomenclature or addition of newly described genera and species.

B. DATA

Data sources

Dung beetle data used in the atlas were drawn from (1) a web-based catalogue of species, (2) museum records, and (3) both published and unpublished field records for distribution and ecological associations. (1) Web-based species data were drawn from the Catalogue of Life (Schoolmeesters 2017). (2) Museum records were drawn from three extensive, local, reference collections during digital databasing (see pg. 2). These were those of (A) the Ditsong (formerly Transvaal) Museum (DM), (B) the National Collection of Insects (NCI), and (C) the Scarab Research Group at the University of Pretoria (UP – now part of the reference collection at the Iziko South African Museum in Cape Town). (3) Most qualitative field data were drawn from unpublished observations of soil, vegetation and food type made between 1970 and 1986 by personnel of the Australian CSIRO Dung Beetle Research Unit (DBRU) based in Pretoria. Most quantitative field data were drawn from unpublished or published studies

made on regional and local dung beetle faunas of South Africa and Botswana between 1983 and 2016 (see list under **Field surveys**).

Digital database

Identities of dung beetles from the reference collections of the three museums (DM, NCI, UP: see **Data sources** from pg. 1) were validated to species level and the information on attached labels was digitised. The species included in the database were restricted to those with validated published names. Information was derived from examination of 91 225 museum specimens in total. The database has been uploaded onto the website of the Animal Demography Unit at the University of Cape Town (click on dung beetle icon at: http://vmus.adu.org.za/) and will also be available on the website of the South African National Biodiversity Institute (SANBI). These records for 555 species (two synonymised post 2017) form the core distribution data used for 542 species accounts in this dung beetle atlas and assessment of conservation status.

Data usage

The data were used in various ways. The web-based catalogue was used to support the cited species names and their overall geographical range across countries of Africa. Museum locality records were used to plot geographical distributions across the target countries of South Africa, Botswana and Namibia as well as most of Zimbabwe and the extreme south of Mozambique. Dates of collection for museum specimens and field data were used to assess months of activity by adults. Quantitative field survey data were used to augment plots of geographical distribution and to assess habitat, trophic and temporal associations in studied species. Qualitative field survey records (DBRU) were used for comparison or support of quantitative data, or as the sole assessment of associations shown by poorly studied species.

Field surveys

Field surveys provide locality records for plotting geographical distributions and environmental records for assessing ecological and temporal associations of dung beetle species within southern Africa south of 15°S. The records comprise both unpublished and published data and are cited liberally in many species accounts using the initial expressions quoted in the brief descriptions below. In these citations, whole numbers represent totals, decimal fractions represent averages per sample.

Unpublished data (mostly South Africa)

1. 'DBRU collection records': Qualitative data derived from observations of soil, vegetation and dung types at > 2 330 dated collection localities contained in the dung beetle reference collection of the DBRU (see pg. 1 in **Data sources**). This collection is now part of the NCI and the locality records form part of the digital database (1970 to 1986).
2. 'In Western Cape' or 'in SW Cape': Quantitative data recorded to cattle dung over one year on different soil and vegetation types at 11 survey sites on farms and reserves near Cape Town ('In Cape of Good Hope Nature Reserve'; Farms: 'At Bonne Attente, Modderrivier, Geelbek, Waylands, Oranjefontein, Pampoenvlei or Groote Post') (1987 to 1988).
3. 'In Ithala Game Reserve': Quantitative data recorded on sandy loam at different altitudes (450–1 320 m) in different vegetation types (forest, shrub/woodland, grassland) using three different dung types (cattle, horse, pig) (KwaZulu-Natal) (1999).
4. 'Near Carolina': Quantitative data recorded to cattle dung on the farm Foggy Valley near Carolina (Mpumalanga) from finer-grained soils in natural, *Themeda*-dominated grassland, regenerating fallow crop fields, and improved Kikuyu pasture (2001 to 2002).
5. 'At Viljoenskroon': Quantitative data recorded to cattle dung on sandy soils of Farm Huntersvlei near Viljoenskroon (N Free State) in a crop field (sorghum), exotic grassland pastures (*Eragrostis*, Smuts finger) and natural grassland (2002).
6. 'On Mariepskop': Quantitative data recorded from two dung types (cattle, pig) on finer-grained soils in natural grassland or forest on the E escarpment of Mpumalanga (2004).
7. 'At Wolkberg': Quantitative data recorded from two dung types (cattle, pig) on finer-grained soils at different altitudes in natural grassland or forest of Lekgalameetse Nature Reserve (Limpopo) (2005).
8. 'In Maputo Special Reserve': Quantitative data recorded to pig dung on deep sands in Maputo Elephant Reserve (S Mozambique) from grasslands of fossil lagoons, coastal dune forest, and small, medium or large sand forest patches (2006).

Published data (mostly South Africa)

1. 'At Bushlands Halt': Quantitative data from coastal KwaZulu-Natal for succession on dung over time

(Doube et al. 1988) and associations with two soil and vegetation types (Giller & Doube 1994).

2. 'Measured...flight activity': Experimental measurement of flight periodicity in some *Onitis* species (Caveney et al. 1989).

3. 'In uMkhuze Game Reserve': Quantitative habitat data for four soil types and two categories of vegetative cover in uMkhuze Game Reserve (Doube 1991) summarised as means per sample in Appendix B.8. of Dung Beetle Ecology.

4. 'Along a gradsect (500 m to 2 800 m on latitude 29–30°S)': Quantitative data recorded at 400–500 m intervals from coastal hills across the Highveld to the top of Sani Pass in KwaZulu-Natal/Lesotho, primarily in grassland on sandy clay loam. Data reported as means per sample by Davis et al. (1999a).

5. 'At Richards Bay': Quantitative data recorded across a post-mining chronosequence of regenerating vegetation (grassland, to dense woodland to open understorey woodland to natural coastal dune forest) reported as totals per vegetation type (Davis et al. 2002) or means per sample in supplementary tables stored on the journal website (Davis et al. 2013).

6. Genus *Pachysoma*: Field observations reported by Harrison et al. (2003).

7. 'At SA Wildlife College': Quantitative data for two soil types in the Kruger National Park and nearby farm rangeland summarised as means per sample (Davis et al. 2012).

8. 'In Botswana': Quantitative habitat (Tshikae et al. 2013a) and trophic data (Tshikae et al. 2013b) from deep sands along a 1 100 km gradsect from the mesic NE (Chobe National Park) to the arid SW Botswana Kalahari summarised as total numbers for six localities or five food types in supplementary tables stored on journal websites.

9. 'At Phalaborwa': Quantitative data for habitat (seven categories), trophic associations (three dung types) and short-term temporal responses to weather conditions (three different) (Davis et al. 2014) cited as totals in a supplementary table stored on the journal website.

Mixed data (South Africa)

1. 'In Gauteng' or 'in Gauteng bushveld': Quantitative data for diel periodicity (Davis 1996a), seasonal activity (unpublished; 1983 to 1984), or associations with six habitat types near Pretoria (Davis 1996b). Habitat and seasonal data recorded over one year. Habitat summarised as total numbers across two soil and three vegetation types.

2. 'In Abe Bailey NR', 'Leeuwfontein NR', 'Roodeplaat NR', 'Suikerbosrand NR', 'Telperion NR' or 'Tswaing NR': Quantitative data derived from different altitudes on different soil and vegetation types forming part of a quantitative survey of six Gauteng nature reserves. Data derived from raw unpublished records or means per reserve in Davis et al. (2005).

3. 'In Northern Cape': Quantitative data from observations of soil type across five defined regions (Davis et al. 2016) with mean numbers per soil type derived from unpublished raw data or mean data per region cited in a supplementary table stored on the journal website.

C. TAXONOMY

Nomenclature has been thoroughly checked. Subfamily, tribal and generic names are mostly based on recent reviews of their validity (Smith 2006, 2009; Branco et al. 2007, 2011; Bouchard et al. 2011). Species names are mostly those listed by the Catalogue of Life (Schoolmeesters 2017) as 'Accepted species' or as published synonyms. They are, therefore, considered relatively well-validated on the assumption that we have correctly matched the species names with reference material used to map distributions. Furthermore, the names listed by Schoolmeesters are regularly updated to remove errors, accommodate revisions and add newly described taxa. Nevertheless, some of the included species and/or their synonyms require further investigation. During databasing, it has become clear that a number of uncorrected errors persist after over two centuries of work on the systematics and taxonomy of the southern African dung beetle fauna. The greatest number of errors occurs in the Onthophagini, which is the largest tribe. It, thus, includes the greatest number of species omitted from the book because of doubtful taxonomic identity. A total of 49 currently valid species described from South Africa, Botswana and/or Namibia could not be reliably matched to reference material. Available information on these species is provided in a separate section entitled **Poorly known species**. A further eight *Onthophagus* species were not considered as their recorded occurrence in South

Africa, Botswana or Namibia could not be validated. Additionally, no consideration was made of many other primarily onthophagine species as they probably remain undescribed and thus lack valid names.

Although most included species are considered reasonably well-validated, possible taxonomic or nomenclatural problems are recorded in about 10% of the species accounts. These possible problems are variously dealt with as either single species or putative complexes of two or more species on the same page. Unresolved problems include: valid species names synonymised in error; synonymous species names that deserve the status of valid species; type series containing more than a single species; undescribed or described species misidentified in the published literature.

A start has been made to revising the alpha taxonomy by describing new taxa and correcting errors. So far, effort has concentrated mainly on the tribe, Scarabaeini although new species have also been described in other tribes since 2017 (see Preamble). However, many more years of work are required to revise the entire membership of the subfamily Scarabaeinae in the subcontinent. Thus, the species included in this book probably comprise only an estimated 80%, or so, of the scarabaeine fauna of South Africa, Botswana and Namibia.

Valid names and synonyms

Most species accounts are headed by the valid species name together with the author and year of description. They are followed by synonyms listed chronologically under the generic name used in the original description. Many names have since changed, particularly those described before 1900. In a few cases, names of synonyms head the species accounts where it is considered that revision would result in formal revalidation. The absence of synonymous names is marked as 'No synonyms'.

There are five different classes of synonyms.

1. Subsequent redescriptions of the same species under different species names.
2. Invalid duplication of names already used for different species in the same genus at an earlier date requiring creation of a new replacement name (*nom nov.*).
3. Citations of species described by earlier authors that were misidentified by later authors. Such species misidentifications are marked as *sensu* the author responsible for the error following the name and author of the cited species, e.g. *Sebasteos westwoodi* (Harold, 1869a) *sensu* Péringuey, 1908, which is a synonym of *Scarabaeus geminogalenus* Davis & Deschodt, 2016.
4. Synonyms containing more than one species in the type series. Such names are marked as '*pars*', e.g. *Phalops adspersipennis* Boheman, 1857, *sensu* Péringuey, 1901 (*pars*), of which only part of the type series is a synonym of *Phalops rufosignatus* van Lansberge, 1885a.
5. Dung beetle species showing different irridescent colours (cupreous, green or blue) produced by multilayer interference within the exoskeleton. In the past, such intraspecific variation was often recognised with published names, e.g. *Onthophagus* (*Phalops*) *ardea* Klug, 1855, var. *chloritus* d'Orbigny, 1902. However, these varietal names are now recognised as synonyms of the original species description, e.g. the green var. *chloritus* d'Orbigny, 1902, is a synonym of the cupreous *Phalops ardea* (Klug, 1855) (see Schoolmeesters 2017: Catalogue of Life).

Photographs

A representative photograph is provided for each species. Because of space limitations, it has been possible to develop only a limited photographic library. This is not a problem with species that show minor external sexual dimorphism. However, many taxa show minor to extreme dimorphism coupled with great morphological variation according to body size (Figure 1). This means that the featured photographs of so-called major males are not necessarily a good guide for identifying all individuals of a species in six of the nine scarabaeine tribes represented in Africa. Although photographs of major females are also provided for those species showing the most extreme sexual dimorphism, there is insufficient space to depict the full range of morphological variation shown by such species.

The photographs may be a reliable identification guide for most species in the Canthonini, Scarabaeini and Gymnopleurini, as they usually show minor external differences between the sexes. The photo images are also helpful for identifying species in the tribes that mostly show limited sexual dimorphism (Ateuchini, Sisyphini). Female images are provided especially for those species in tribes that include genera or species groups showing extreme sexual dimorphism, i.e. a few Onitini and Oniticellini plus many Coprini and Onthophagini, particularly in the genera: *Copris*, *Catharsius*, *Heliocopris* and some *Proagoderus* plus *Onthophagus*.

The wide range of morphological variation in sexually dimorphic species is correlated to body size. Depending on the taxon, horns and sculpturing on the head, protuberances on the prothoracic disc and/or shape and dentition of the legs, show great prominence in larger-bodied, major males and females. These features change in shape and

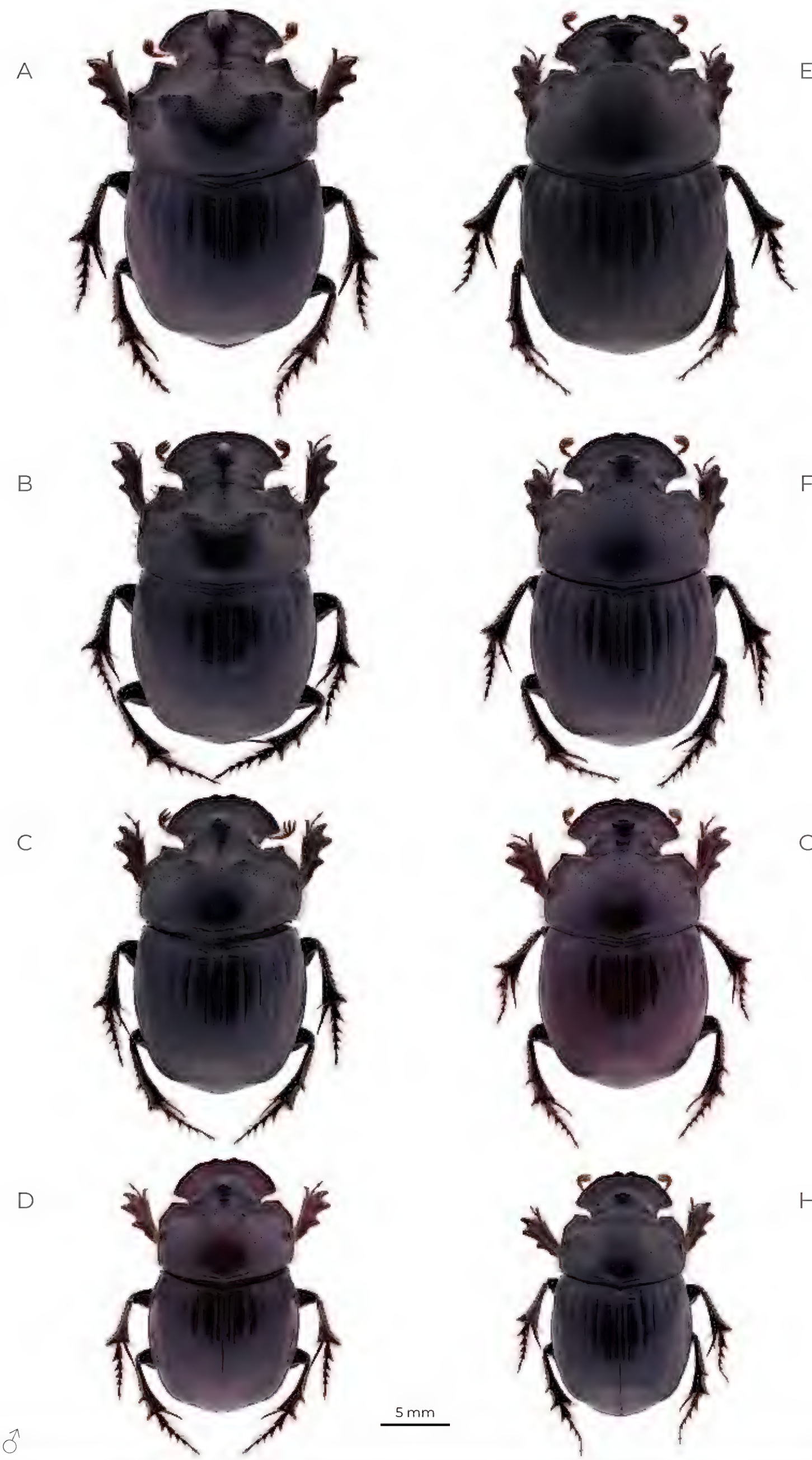


Figure 1. Extreme morphological variation related to body size in *Copris elphenor* Klug, 1855. So-called major to minor males (A–D) and major to minor females (E–H).

decline in prominence with smaller body size to a point where minor males and females may be close to one another in appearance (Figure 1). Plots of body size against size of secondary sexual armature generally describe a sigmoid curve (Moczek 2002). The switch from major to minor features, thus, occurs over a relatively small range in body size.

The taxonomy section in each species account identifies sexually dimorphic species with an indication of the body parts involved (head, prothoracic disc and/or legs). Species showing colour or colour pattern variation are also identified together with an indication of the nature of differences, particularly in iridescent species (cupreous, green and/or blue).

Type localities

Type localities are listed in chronological order for species and synonyms, if any. Where a holotype was designated, a single locality is cited. Where status of types was not specified, they are regarded as syntypes and all localities are cited. Species names and localities are as quoted in the original published descriptions. Where clarification is required, modern name changes to localities follow in square brackets along with any necessary qualifying comments. Sometimes, subsequent publications create lectotypes or neotypes if original type material was inexactly designated or has been lost. In such cases these lectotype or neotype localities are also quoted. It should be noted that subsequent publications sometimes cite original type localities according to all of the listed names, the first listed name, or that on the locality labels of type specimens. Thus, in some cases, original type localities cited here may differ from those cited in later published descriptions.

Type localities may be useful for assisting validation of species names. However, for many older types, localities were not stated with the original descriptions or they are particularly inaccurate, ambiguous, or even erroneous. Some of the recurring inaccurate type localities cited in the late 18th and early to mid-19th centuries comprise: *Cape of Good Hope* (in various formats and languages), *Caffraria* (sometimes followed by *tota*, *interiore* or even *Ngami*), *in terra Natalensi*, *juxta fluvium Limpopo* or *juxta fluvium Gariep* [KwaZulu-Natal, near Limpopo River, or near Orange River]. Caffraria is a particularly abused citation. In the narrowest sense, it comprises a section of the SE coastal region from the Eastern Cape of South Africa to southern Mozambique (see species account for *Kurtops caffrarius*), but dung beetle distribution data suggest it has often been used much less exactly for southern Africa in general or any area therein.

D. DISTRIBUTION DATA AND METHODS

Dung beetle distribution data have been treated in various ways. Species distributions have been outlined on a map for the whole of Africa and plotted as data points on a customised map panel for southern Africa. They have also been described according to occurrence in African countries (Schoolmeesters 2017) and coincidence with vegetation regions of South Africa (Mucina & Rutherford 2006) or ecoregions of Namibia, Botswana, Zimbabwe and the extreme south of Mozambique (Olson et al. 2001). Locality data for southern Africa south of 15°S have also been used to calculate climatic associations (altitude, rainfall, temperature).

Geographical range

The overall geographical range of each species in Africa has been determined from two sources: (1) countries of occurrence derived from publications (Schoolmeesters 2017); and (2) available distribution data. These data are often less than ideal. The range represented by listed countries is divided into validated occurrences, non-validated citations and likely errors resulting from mistakes in the published literature. Measurements of EOO (Extent of Occurrence) vary from fairly accurate to gross estimates for species with the largest ranges. Except for Kenya and northern Tanzania, validated data were severely limited for species with distributions continuing north of 15°S. Except in cases where a species is known from only a single locality, a map of Africa showing the overall geographical range has been placed as an inset into the map panels for species distribution in southern Africa (Figure 2). In general, ranges varied from very large to very small with the latter bias variously representing (1) natural localisation due to specialisation, (2) range fragmentation due to loss of preferred vegetation or dung types, or (3) a collection artefact.

Distribution in southern Africa

Distribution data for each validated species recorded in South Africa, Botswana and Namibia, were plotted onto a customised map for southern Africa that primarily encompassed an area south of 17°S and west of 33°E (Figure 2). The map panel also included Lesotho and Swaziland

(now Eswatini), most of Zimbabwe, and small parts of Mozambique, Angola and Zambia. For each species, distribution was plotted onto the map panel as presence within ~15 × 15 km^2 squares that represent the subdivision of degree squares of latitude and longitude into 16 ~equal parts. Most distributions are plotted using red squares although other colours are used (black, blue, green, grey) where (1) more than a single taxon or single putative taxon are plotted onto a single map, where (2) there is overlap between multiple taxa, or where (3) some records are questionable.

Based on mapped distributions, 281 species have been classified as endemic since available data were restricted to one (228), two (31) or all three of the focal countries of South Africa, Botswana and Namibia (22) (Table 1). Of these species, a total of 200 are recorded as solely South African endemics. A further 261 species are not marked as endemic, since their ranges extend beyond the borders of any one, two or all three of the target countries.

Locality data for southern Africa

The ranges shown by each species in southern Africa have been summarised in terms of altitude (m), annual rainfall (mm) and annual temperature (°C: max. + min. / 2). These data have been extracted from GIS base maps comprising interpolated average climatic data for 5 × 5 km polygons using spot grid references for all specimens recorded from S of 15°S. This includes data for specimens recorded in the areas laying outside of the map panel boundaries between 15 to 17°S and 33 to 35°E. For species known from more than a single locality, these data are expressed as a mean ± SD and a range. The data comprise only one value per 5 × 5 km polygon in order to reduce the effects of asymmetrical collecting intensity across southern Africa.

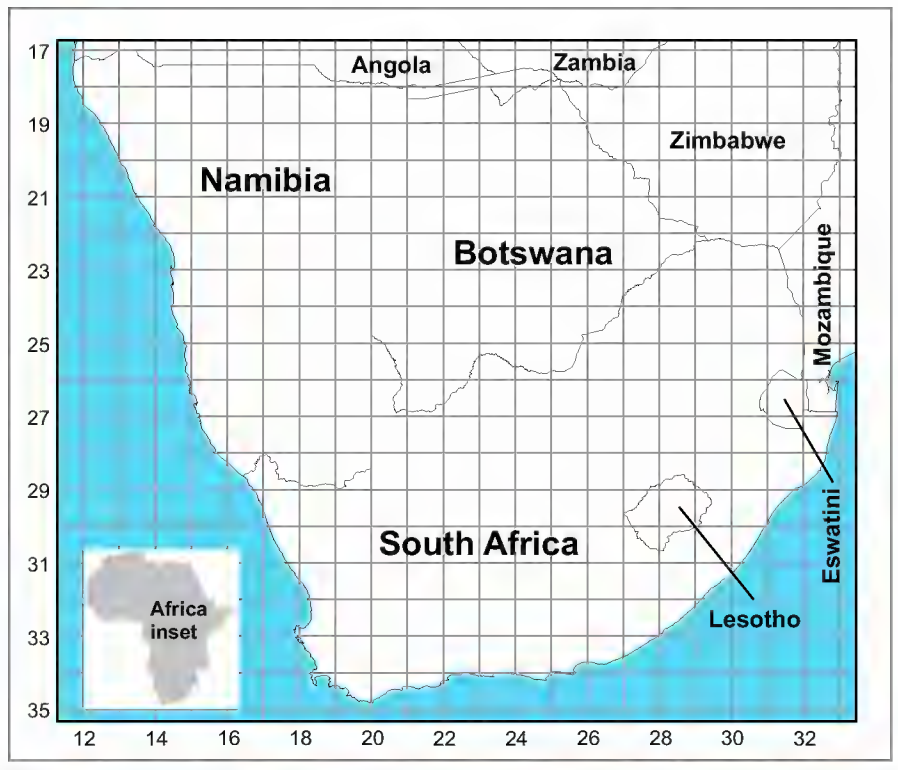


Figure 2. Map panel of southern Africa onto which spot distributions (1/16th degree squares) were plotted for each species within an area delimited by 17°S and 33°E; inset onto which range within Africa was superimposed for species with more than a single geographical record.

Reliable distribution data are derived from three sources:

1. Localities derived from validated, databased museum records.
2. Localities in South Africa and Botswana derived from validated raw data in unpublished and published studies that are cited in the **Field surveys** section.
3. Validated locality data derived from recent, published, taxonomic revisions, particularly in the tribes, Canthonini and Ateuchini.

In general, the data for South Africa was the most comprehensive (see **Synthesis** section) although there were also good records derived from serial collections and quantitative work in Botswana and Namibia. Good data were also available for the extreme south of Mozambique, but those for Zimbabwe were much more limited.

Climatic associations

The climate of southern Africa is influenced by temperature variation related to a latitudinal gradient from 34°S to 17°S, variable topography, and differences in the amounts (<100 to >1 500 mm) and seasonality of annual rainfall.

In general topographical terms, the subcontinent is bordered by a relatively narrow strip of coastal lowlands delineated by mountain ranges. The Cape Fold Mountain Belt borders the south coast whereas the east and west coasts are bordered by mountain escarpments that define a central plateau, which is tilted from high altitude in the east to lower altitude in the west (Partridge & Maud 1987; Maud 2012). Across this area, two cells of wind currents show seasonal expansion bringing, respectively, winter rainfall from the Atlantic Ocean to the southwest and summer rainfall from the Indian Ocean to the northeast (Tyson 1986). Furthermore, upwelling of cold glacial waters result in a cell of dry air and a desert climate on the West Coast. The adjoining central parts of the subcontinent also have an arid climate as the sequential expansion of air currents bringing rainfall only reach the area late in each rainy season. Thus, the subcontinent may be divided into four major climatic regions (Walter & Lieth 1964).

1. Winter rainfall region in the cooler southwest.
2. Bimodal spring/autumn rainfall region along the cooler south coast.

3. Arid late summer rainfall region on the cooler northwest coast and hotter west to south centre.
4. Mid-summer rainfall region in the cooler highlands and warmer lowlands to the more mesic northeast.

Numbers of dung beetle species in South Africa show a decline from the northeast to the southwest (Davis 2002). Previously, a combined total of 386 species has been recorded to the northeast in the mid-summer rainfall region. Although northeast sub-regions show smaller totals, there are still around 150 species in the highlands or greater than 200 in the lowland sub-regions. This number is reduced to around 125 species in the central arid late summer rainfall region (Davis et al. 2016). In the bimodal rainfall region of southern South Africa and the winter rainfall region of the southwest, respectively, only 86 and 62 species were previously recorded (Davis 2002). Numbers cited by Davis (2002) are updated in the **Synthesis** section.

Bioregions and ecoregions

Coincidence of dung beetles with defined ecological regions assists in assessment of conservation status. It was decided to use two different classification systems: one for vegetation types in South Africa (Mucina & Rutherford 2006) and one for the remainder of southern Africa that comprised part of a global classification of ecoregions (Olson et al. 2001).

The vegetation of South Africa has been classified at three different spatial scales using regression trees (Mucina & Rutherford 2006). From larger to smaller scales, these comprise eight biomes (Figure 3), 35 bioregions and 439 vegetation units. Principal associations of dung beetles with vegetation areas have been described according to the size of their ranges. Those showing larger ranges are mostly described at biome and bioregion scales. Those showing

Table 1. Numbers of species assessed for the IUCN Red List; numbers of endemic species and numbers also recorded outside of the borders of South Africa, Botswana and Namibia; numbers of species assessed for each IUCN threat category (see IUCN 2001)

CATEGORIES	Number of species accounts (% of total species accounts) per tribe																	
	Ateuchini		Canthon.		Coprini*		Gymnopl.		Oniticell.		Onitini		Onthoph.		Scarab.		Sisyphini	
IUCN Red List	4		15		9		7		6		13		25		23		8	
Endemic status																		
South Africa (RSA)**	16	(55)	64	(78)	34	(40)	2	(10)	2	(8)	10	(22)	33	(24)	28	(30)	10	(38)
Namibia	0		12	(15)	3	(4)	1	(5)	0		2	(4)	1	(1)	8	(9)	0	
Botswana	0		0		0		0		0		0		0		1	(1)	0	
RSA/Botswana	0		0		2	(2)	0		0		0		1	(1)	4	(4)	0	
RSA/Namibia	0		2	(2)	0		0		0		7	(16)	3	(2)	10	(11)	1	(4)
Namibia/Botswana	0		0		0		0		0		0		1	(1)	1	(1)	0	
RSA/Namibia/Botswana	1	(3)	1	(1)	6	(7)	1	(5)	0		2	(4)	2	(1)	9	(10)	0	
Total endemics	17	(58)	79	(96)	45	(53)	4	(20)	2	(8)	21	(46)	41	(30)	61	(66)	11	(42)
Not endemic	12	(42)	3	(4)	40	(47)	16	(80)	24	(92)	24	(54)	95	(70)	31	(34)	15	(58)
Conservation status																		
Data Deficient (DD)	16	(55)	41	(50)	24	(28)	4	(20)	5	(19)	15	(33)	26	(19)	26	(28)	5	(19)
Least Concern (LC)	12	(41)	25	(31)	56	(66)	16	(80)	21	(81)	28	(62)	110	(81)	62	(67)	20	(77)
Near Threatened (NT)	0		0		3	(4)	0		0		1	(2)	0		1	(1)	1	(4)
Vulnerable (VU)	0		15	(18)	0		0		0		1	(1)	0		2	(2)	0	
Endangered (EN)	1	(3)	1	(1)	2	(2)	0		0		0		0		1	(1)	0	
Critically Endangered (CR)	0		0		0		0		0		0		0		0		0	
DD but ?threatened																		
DD/NT	0		1		0		0		0		0		1		1		0	
DD/VU	5		9		8		0		0		1		0		4		1	
DD/EN	2		4		3		0		0		1		0		2		0	
DD/CR	2		1		0		0		0		1		0		0		0	
Total N species accounts	29		82		85		20		26		45		136		92		26	

**Catharsius bradshawi* not included

**Includes Lesotho and Eswatini (formerly Swaziland): nine in RSA/Lesotho; five in RSA/Eswatini; one canthonine in Eswatini only.

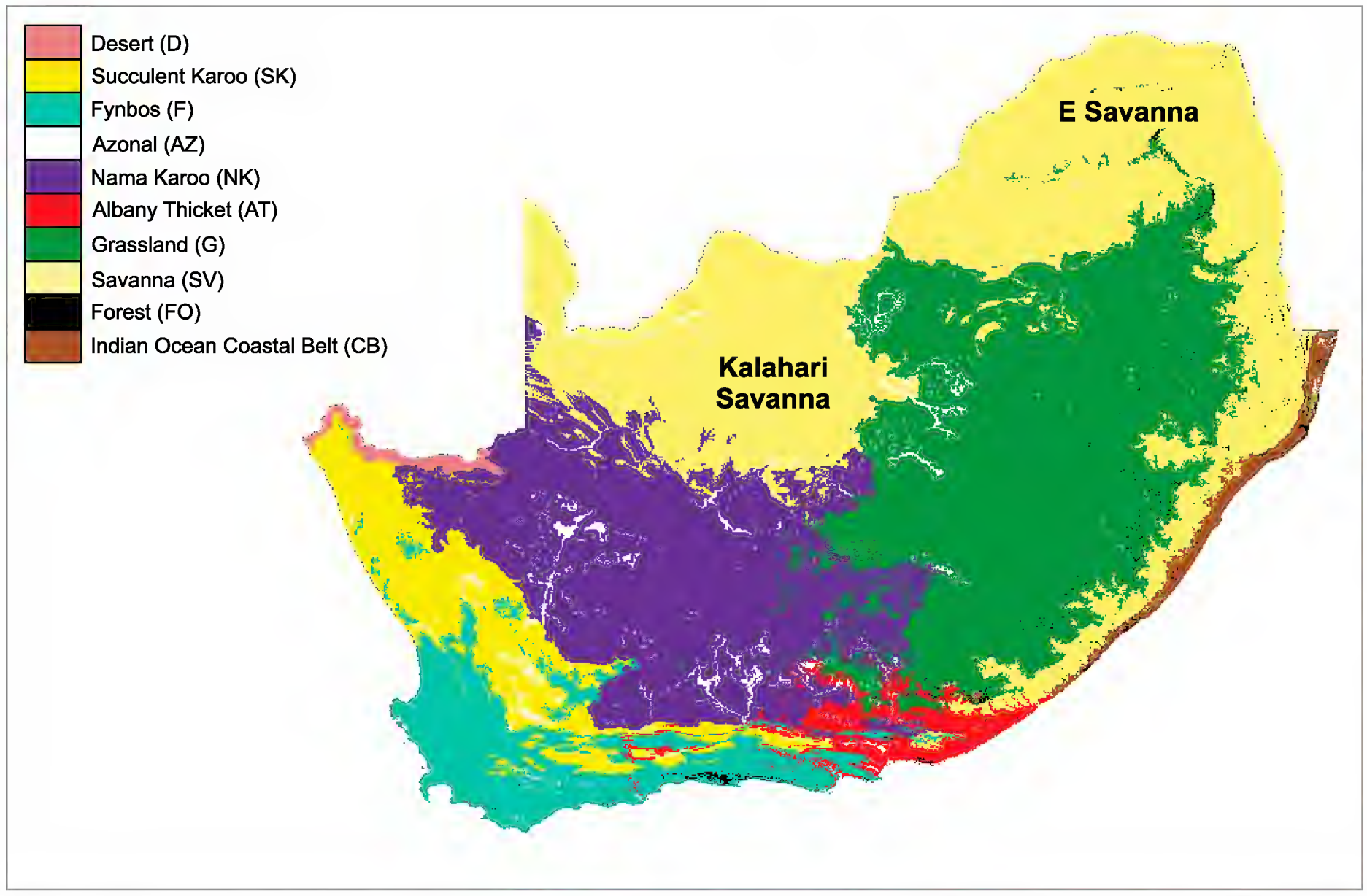


Figure 3. Map showing the vegetation classification for South Africa (Mucina & Rutherford 2006) at biome scale.

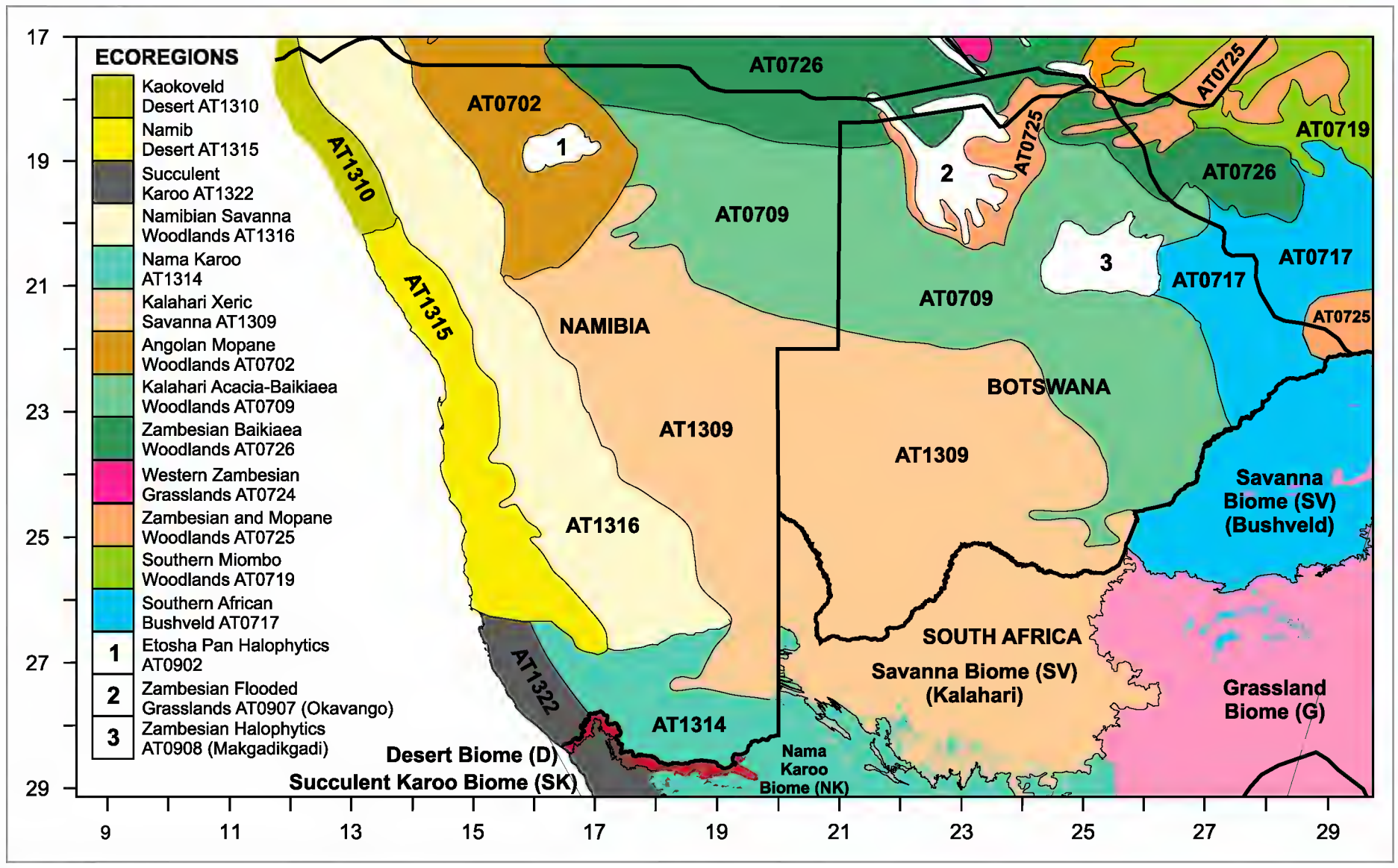


Figure 4. Map showing (1) the ecoregions of Namibia and Botswana plus parts of Angola, Zambia and Zimbabwe (Olson et al. 2001: Arid: AT1309–1322; Savanna: AT0702–0726; Lacustrine: AT0902–0908) and (2) how they abut onto the vegetation classification for South Africa at biome scale (Mucina & Rutherford 2006).

smaller ranges are also described at vegetation unit scale within the context of both bioregion and biome scales. Statements on the proportional modification of biomes, bioregions and/or vegetation units plus its potential impact on conservation status have been provided for many species whose ranges partly or wholly coincide with highly modified and/or fragmented natural vegetation cover.

Although the ecoregion classification of Olson et al. (2001) is global in extent, it has been used to describe dung beetle distribution only in Botswana, Namibia, most of Zimbabwe and the extreme south of Mozambique (Figure 4). Distributions are described for 11 principal ecoregions defined across that area. Except in the case of the north Botswana alluvial soil specialist, *Escarabaeus remii*, there are no records from three sizeable ecoregions of alluvial soils comprising Etosha Pan (Namibia), Okavango Swamps and Makgadikgadi Pan (N Botswana). Furthermore, no data are provided for the 14 ecoregions recorded across South Africa as descriptions of distribution across the vegetation regions of Mucina & Rutherford (2006) are considered more comprehensive.

E. ECOLOGICAL ASSOCIATIONS

Dung beetles show a range of ecological associations from relatively generalist to relatively specialist. Therefore, identification of preferred habitats (soil and vegetation types) or preferred food (primarily carrion, fungi, millipede body contents or dung type) is important for conservation purposes. Identification of factors that contribute to the observed associations are also important.

Soil type

As fossorial insects, dung beetles are strongly influenced by the textural (Davis 1996b) and hydrological properties of soil. Associations with soil type are mostly defined using four categories from the soil texture, classification system (sand, sandy loam, sandy clay loam, clay) of the United States Department of Agriculture (USDA). In rank order, this classification represents contrasting grain size profiles from coarse to increasingly finer-grained, which vary according to proportions of sand, silt and clay in each soil type. Ease and depth of tunnelling varies with soil type (Hanski & Cambefort 1991a). It increases across the gradient from finer to coarser-grained soils and also with increasing soil moisture content following rainfall. Species richness and biomass of dung beetle assemblages tends to be greater on sandy soils than on finer-grained soils (Davis 1996b).

Influences of grain size profiles on soil hydrological properties include faster rate of drainage on coarser sandy soils and higher water retention capacity in finer-grained soils. Such properties are modified by dung beetle tunnelling activity (Brown et al. 2010). Variation in soil hydrological properties according to grain size may be associated with differences in survivorship of immatures of different species on different soil types (Fincher 1973). Differences in water content between drier and moister soils may also influence nest architecture (Rougon & Rougon 1982). Associations with textural categories of soil type have been provided for each species where available.

Vegetation type

Dung beetles are strongly influenced by structural properties of vegetation at both macro- and microhabitat scales. Macrohabitat associations with different vegetation types have been defined primarily in terms of (1) increasing height of the vertical profile from grassland to forest and (2) increasing cover density of the canopy in woody vegetation. In terms of the surface microhabitats occupied by dung beetles, this represents a gradient from exposure to radiant heat to potential protection by increasing shade. Such differences in the surface microhabitat are known to strongly influence species representation and assemblage structure of dung beetles (Davis et al. 2013). Vegetation associations are, therefore, described in terms of (1) grassland and scrub, which provide little shade, (2) open shrubland or woodland, which may provide partial shade, and (3) dense woodland, thickets or forest, which provide the greatest shade.

Vegetation type is also responsible for creating or enhancing the surface microhabitats favoured by species. For instance, a number of small-bodied specialists is associated with the carpet of leaf litter found in forests. Furthermore, dung beetle activity is favoured by greater density of surface cover in grassland (Jankielsohn et al. 2001), which reduces surface evaporation. However, extreme surface cover density in fertilised Kikuyu pasture may inhibit tunnelling activity (Davis et al. 1999). Also, the importance of shade is illustrated by observations on the effect of weather conditions. On cloudy days, the shade specialist (*Sisyphus nanniscus* cited as *S. costatus*) has been recorded in abundance in tall grass 50 m from dense woodland thicket (Doube 1983). Associations with categories of

vegetation type and particular microhabitats (if applicable) have been provided for each species where available.

Food type

Although association with mammalian dung dominates in the subfamily Scarabaeinae, various other specialist associations occur, including those with carrion, fungi and millipede body contents. In the dominant dung-associated component, many species show a bias to particular dung types (Davis 1994; Davis et al. 2014) that differ according to mammalian body size, diet and digestive processes. This results in dung types that vary in volume, physical consistency and spectra of released volatiles (Dormont et al. 2010) to which dung beetles are attracted by olfaction (Shibuya & Inouchi 1982; Inouchi & Shibuya 1986). Therefore, proportional associations with dung or other food types have been provided where available. However, some citations merely list mammals from whose dung collections were made. These citations may categorise mammals according to diet and digestive process: (1) carnivores or omnivores producing small strong smelling droppings; (2) ruminant herbivores producing pellets or large fine-fibred pads; (3) monogastric herbivores producing large coarse-fibred droppings.

F. TEMPORAL ASSOCIATIONS

Temporal associations may have little relevance for current conservation purposes although drivers of such patterns may be important, particularly in a future threatened by climate change. Temporal activity is described at three different scales, (1) diel (variation over 24 hours of each day), (2) day-to-day variation according to weather conditions and (3) seasonal. The joint effects of activity at these temporal scales may contribute to long-term, year-to-year changes in diversity that should be monitored under a scenario of climate change.

Diel periodicity

If known, diel periodicity is classified as either diurnal or active under darkness. Additional notes are added for a few species for which more detailed, quantitative data on daily activity peaks is available. The diel patterns are driven by light intensity and temperature (Caveney et al. 1989).

Short-term weather responses

Dung beetle activity varies from day-to-day depending on incidence of favourable or unfavourable weather conditions for activity (Davis 1995, 2002). During seasonal peaks in activity, variation is primarily mediated by incidence of substantial rainfall and incidence of cloud cover, which affect diel cycles of temperature and light intensity. Rainfall also increases the ease with which soil may be tunnelled. As long as temperatures are sufficiently high, numbers of active species increase after substantial rainfall and decline during periods of dryness (Davis 1995, 2002). Over a 10-day period in early summer that commenced with heavy rainfall and progressed to warmer drier weather, the number of active species in grassland on sandy clay loam declined from over 40 to around 20 in the Gauteng bushveld (Davis 2002).

Seasonal activity

Although seasonal peaks in activity are described for only some species where quantitative data are available, a qualitative assessment of annual activity is provided for all species by shading along a bar graduated in months. Such data are derived from months of collection on locality labels of reference material and from raw data of quantitative studies. Most of these assessments are probably representative of the annual pattern of activity. However, it should be noted that there may be some bias as most collecting trips have been mounted in the warmer parts of rainy seasons, which are much more favourable for activity than the unfavourable cool and/or dry seasons. It should also be noted that chance records of single specimens under unfavourable, out-of-season conditions have the same weight as many specimens recorded during seasonal peaks in activity. The recorded extent and patterns of seasonal activity may even vary according to different climatic conditions across a species range.

Overall, seasonality of dung beetle activity varies according to the different rainfall patterns in the four main climatic regions of southern Africa (see under Climatic associations pg. 7). In the summer rainfall region to the northeast, rainfall usually coincides with warmer temperatures leading to a unimodal mid-summer peak in dung beetle activity (Davis 2002). In the winter rainfall region to the southwest, rainfall usually coincides with cooler temperatures, leading to bimodal peaks in dung beetle activity during the warmer spring and autumn.

Year-to-year activity

Dung beetle activity varies substantially from year-to-year in terms of relative abundance of species (Doube 1991). Although the reasons have not been established, year-to-year differences in the frequency of rainfall events would influence activity patterns of different species and their breeding opportunities. Between-species differences in breeding success would drive different patterns of diversity in the following year. Under a scenario of long-term changes in climate, such responses would have implications for conservation, particularly for species with small ranges showing ecological specialisations.

G. CONSERVATION STATUS AND METHODS

For assessments of conservation status, we use the categories recommended in the IUCN Red List, Version 3.1 (IUCN 2001). As trends in population dynamics are mostly unknown, awarding of categories is largely based on spatial distribution patterns using the rules stipulated for range size and number of known locations (IUCN 2001: see below). However, assessments may also be modified after a consideration of ecological associations and representation in reserves, if known.

Assessment rationale

The starting point for each assessment is a measurement of the Extent of Occurrence (EOO) derived from an outline of available validated distribution data that are, in some cases, severely limited. This is usually only an estimate of actual occurrence as an Area of Occupancy (AOO) is generally unavailable. However, available ecological data may provide insight into likely influences on spatial frequency, range restriction or range contraction within the cited EOO. Generalisation versus specialisation to soil type may be influential if an association results in a small range. Restricted occurrence of preferred vegetation types or coincidence with areas of highly modified vegetation structure are particularly pertinent to the conservation status of dung beetles. Data on proportional transformation of vegetation units within bioregions (Mucina & Rutherford 2006) are sometimes included as a guide to the extent of possible threats to a species. Increasing range restriction of mammals dropping preferred dung types may also be influential and is often identified by a current beetle distribution pattern centred on reserves. Although population data are usually limited, numbers in collections or quantitative sampling may provide insights into relative temporal frequency or rarity. Based on these data, an IUCN threat category is provided.

IUCN categories

As indicated in relevant species accounts, conservation status of 110 taxa found in South Africa, Botswana and/or Namibia has been previously assessed for the IUCN Red List website (http://www.iucnredlist.org/) (Table 1). For each species, the awarded IUCN threat category depends on how much is known concerning its EOO, AOO and ecological associations. A summary is provided below.

1. Data Deficient (DD): Assessment for 160 species for which information is extremely limited. However, threat categories are also discussed for 40 of these species (NT, VU, EN or CR, see below) if they show small or highly fragmented ranges that are clearly not collection artefacts. This would potentially augment the small numbers of species (30) currently awarded threat categories (Table 1).

2. Least Concern (LC): Assessment for the majority of species (350) that show large ranges and high frequency or small ranges with high abundance within reserves. Because Scarabaeinae are primarily coprophagous, the wide availability of dung results in assessments of Least Concern (LC) for many southern African species. Similarly, assessments of LC are also awarded to a number of species with specialisations on other widely available food types, such as carrion, fungi or millipede body contents.

3. Near Threatened (NT): 'A taxon is Near Threatened when it has been evaluated against the criteria, but does not qualify for Critically Endangered, Endangered or Vulnerable now, but is close to qualifying for or is likely to qualify for a threatened category in the near future' (*verbatim* from IUCN 2001); currently awarded to six species.

4. Vulnerable (VU): Threat category awarded if a species shows an EOO < 20 000 km^2, AOO < 2 000 km^2, fragmented range or records from only 6–10 locations; currently awarded to 18 species.

5. Endangered (EN): Threat category awarded if a species shows an EOO < 5 000 km^2, AOO < 500 km^2, fragmented range or only five locations; currently awarded to six species.

6. Critically Endangered (CR): Threat category awarded if a species shows an EOO < 100 km^2,

AOO < 10 km^2, fragmented range or was recorded from only one location; not currently awarded to any species, but the flightless *Copris sexdentatus* (EN) is currently known from only one location in critically endangered Eastern Rûens Renosterveld having been recently re-recorded at one small reserve after a hiatus of many decades.

7. Extinct (EX): No southern African scarabaeine species is currently regarded as globally extinct. However, at the time of writing, two flightless fynbos taxa have not been re-recorded for many decades (*Copris sphaeropterus*) or over a century (*Aphengoecus clypeatus*).

VU, EN and CR categories are considered to represent a high risk of extinction in the wild.

Conservation measures

Conservation measures are recommended for all but a few species. However, information on which to base assessments are often limited to some degree, whatever the awarded threat category. In some cases, further work is required on taxonomic status or geographical range. However, most frequently, there are recommendations for data on ecological associations which may be absent, restricted to qualitative observations, or do not represent sufficiently detailed quantitative support. Without such supporting data it is difficult to determine if the AOO is likely to be smaller than the EOO. Each section ends with citation of a few reserves where the species is protected or a statement that current records of the species are not known to coincide with any reserve.

H. POTENTIAL THREATS

Regional habitat transformation

In Namibia and Botswana, transformation of natural ecoregions (Olson et al. 2001; World Wildlife Fund 2017) is mostly fairly limited except for the moister, more densely populated north and east. Assessments of conservation status are not equivalent to those for South Africa (see below) as they are made in terms of both vegetation and natural mammal complement. Ranges of the latter have been more highly modified than vegetation. Three ecoregions are assessed as relatively stable/intact (World Wildlife Fund 2017), which may equate to least concern (Namib Desert: AT1315; Kalahari Xeric Savanna: AT1309); Zambezian and Mopane Woodlands: AT0725). Five are assessed as vulnerable (Nama Karoo: AT1314; Namibian Savanna Woodlands: AT1316; Kalahari Acacia-Baikiaea Woodlands: AT0709; Southern African Bushveld: AT0717; Zambezian Baikiaea Woodlands: AT0726) (World Wildlife Fund 2017). Woodland clearance is cited as a problem in AT0726, overgrazing by domestic livestock as a problem in AT0709, AT1314, AT1316, with overhunting a problem in AT1316 and all indigenous fauna hunted out in the Namibian part of AT1314. Three ecoregions are assessed as critical/endangered (World Wildlife Fund 2017), which may equate to endangered (Succulent Karoo: AT1322; Kaokoveld Desert: AT1310; Angolan Mopane Woodlands: AT0702). However, this does not apply to the Namibian parts of these ecoregions. In Namibia, AT1322 is protected in the Sperrgebiet National Park where the vegetation is mostly intact although there is disturbance by mining on the coast with fencing preventing mammal migration in the east. Also in Namibia, AT1310 and AT0702 are largely protected by local and national conservancies although poaching is a problem.

In South Africa, conversion of natural environment to urban centres or agro-ecosystems varies from limited to fairly advanced (Mucina & Rutherford 2006). Assessments of conservation status are made in terms of vegetation transformation as the large-bodied members of the natural mammal fauna are now largely restricted to reserves and game farms. Vegetation of the arid regions from central South Africa to the West Coast remain relatively little transformed and are considered least concern (0–20% transformed) (Nama Karoo, Succulent Karoo, Desert biomes; most of the Albany Thicket Biome and Kalahari Savanna bioregions; see Mucina & Rutherford's Figures 3.8 and 16.5). However, the moister Grassland and Savanna biomes to the northeast are largely classified as vulnerable (20–40% transformed) to endangered (60–85% transformed). This excludes the savanna bordering the Limpopo Valley and Kruger National Park, and high altitude areas, particularly the Drakensberg Grassland bioregion, which remain least concern (see Figure 3.10. in Mucina & Rutherford 2006). Similarly, much of the moister east and south coastal regions (Indian Ocean Coastal Belt, Fynbos biomes) are highly modified with assessments varying from vulnerable to endangered or even critically endangered (85–100% transformed) in large, lower-altitude areas of the Western Cape that coincide, particularly with Renosterveld. However, again, many mountainous areas and some sandy south coastal areas in the Fynbos Biome remain assessed as least concern.

The relative influence of habitat transformation on dung beetle species is dependent on the size of their geographical range and the breadth of their ecological associations (generalist or specialist). Species with ranges that coincide with the most modified coastal or northeast regions of South Africa are potentially those most at risk. The degree of risk would increase for species with small overall range and specialist ecological associations, particularly specialisation to threatened vegetation and food types. Threatened vegetation may be associated with particular soil types, such as sands concentrated around much of the coastline or in outliers within savanna, although this does not apply to the sands of the Kalahari Basin, Namib Desert and outliers in the Karoo.

Local habitat modification

Potential threats stem from modification to the natural environment. These may or may not impact on particular ecological associations shown by each dung beetle species.

Soil modification

Widespread only with regard to ploughing.

1. Ploughing: Conversion of natural habitat to arable lands is perhaps one of the most extreme forms of transformation. Although only 10.3% of the land surface of South Africa was transformed as arable lands by 2014, it is the geographical concentration of such farming that is important as a conservation factor, particularly in the Renosterveld of the southwest Cape, to which two, now extremely rare flightless species, are apparently endemic.

2. Mining: In general, mining is usually spatially restricted in its effects although open cast mining is, potentially, more of a threat. Measurements near Phalaborwa indicated limited influences from mining (Davis et al. 2014).

Vegetation transformation or habitat fragmentation

Widely modified for both urban development and farmland in the southwest and northeast of South Africa as well as along much of the coastline.

1. It has been shown that many winter rainfall endemics are associated primarily with the natural shrublands of the fynbos region (Davis 1993). Thus, loss of shruband to arable farming (see ploughing of Renosterveld above), development of grassland pastures and urban expansion is a growing threat to many species in the Eastern and especially the Western Cape.

2. Indigenous forest patches along the coastline and mountain escarpment in the south and east are known to harbour various often rare or uncommon endemic genera and species, most of which are assessed as threatened. These forest patches are naturally restricted in extent. Thus, threats from unsanctioned and uncontrolled clearance, area reduction, degradation and exploitation would be detrimental.

3. A number of savanna species are recorded as showing a bias to thickets or open woodland vegetation (Davis 1996b). Therefore, proportional estimates of transformation and clearance in woody vegetation units provide some insight into potential local threats.

4. Modification of Highveld grass cover by pasture improvement has been little studied although differences have been recorded for some species between dense Kikuyu pasture and less dense natural *Themeda*-dominated grassland (see species accounts with data cited from 'At Foggy Valley').

5. The impact of conversion of Highveld Grassland to tree plantation by commercial forestry has been little measured.

6. Observations suggest that reduction in vegetation cover by overgrazing also influences diversity of dung beetle assemblages in grassland regions. Although it has been little measured, one study has shown a reduction in abundance of larger-bodied species from undisturbed to overgrazed grassland (Jankielsohn et al. 2001).

Food availability and toxicity

Availability of dung types of indigenous mammals is widely modified in southern Africa. Over wide areas, these dung types have been replaced by those of domestic livestock, which may be potentially toxic due to widespread use of pesticide treatments.

1. Range reduction of large indigenous mammals through hunting has lead to loss in availability of particular dung types from most of South Africa and extensive areas of Namibia and Botswana. This has been most influential on those species associated, especially, with antelope pellets on the Highveld and coarse-fibred dung of monogastric herbivores

over most of the subcontinent. Distributions of a number of species are now concentrated in areas containing game reserves with the implication of past contraction in their ranges.

2. Several types of synthetic pesticide treatments are used to control ecto- or endoparasites on the domestic livestock that have widely replaced the large indigenous mammal fauna. These are administered as pour-ons (pyrethroids) or also as ingestables or injectables (avermectins, milbemycins). All leave varying amounts of residues in dung that are variously toxic to dung beetles, both globally and in southern Africa (Davis et al. 2004; Wall & Beynon 2012; Jacobs & Scholtz 2015). Further monitoring of the effects would be advisable.

Range contraction

In summary, range contraction by dung beetles may result from specialisation to particular dung types dropped by mammals that have become range restricted through hunting, the so-called game reserve effect. It may also occur through clearance of woody vegetation that removes suitable conditions for specialists to shady or partially shady conditions. Such effects of habitat degradation may be exacerbated by specialisation to particular climatic or soil type conditions. Ranges of the most threatened species mostly coincide with areas that have undergone extensive to extreme modification due to urban development or farming practices, particularly the southwest Cape, south and east coastline, and northeast South Africa (Highveld Grassland, woody savanna, woody coastal vegetation).

I. USE AS INDICATORS

Scarabaeine dung beetles are used, globally, as an indicator group owing (1) to their sensitivity to habitat heterogeneity and transformation, and (2) ease with which they may be sampled quantitatively using dung-baited pitfall traps (Halffter & Favila 1993; McGeoch et al. 2002; Spector 2006). Therefore, the accuracy of nomenclature and correct identification are important.

In southern Africa, dung beetles have been used to assess patterns of distribution and association at various spatial scales (Davis et al. 2004) from biogeographical down to local habitat and microhabitat. These studies have investigated (1) classification of geographical areas (Davis et al. 2016), (2) habitat and food associations (Davis 1996b; Tshikae et al. 2013b), (3) effects of vegetation type fragmentation (Davis 1993) or restoration including influences of microhabitat (Davis et al. 2013), and (4) effects of food availability or quality as regards range contraction in indigenous monogastric mammals (Davis 1997) or treatment of domestic livestock with pesticides leading to harmful residues in their dung (Kryger et al. 2006, 2007).

J. FORMAT OF SPECIES ACCOUNTS

The book comprises sections on the subfamily Scarabaeinae, the nine tribes found in Africa, and the 86 genera found in South Africa, Botswana and Namibia. It also comprises 542 species accounts for dung beetles found in these three countries. Each species account is arranged according to a standard format of 14 to 15 sections. Depending on geographical distribution, one or the other of sections 12 and 13 may be deleted or both may be included. The content under the headings varies according to the history of the species and the amount of available information.

Species accounts

1. **Species name(s):** Cited in large font italics followed by synonyms (if any) in smaller font italics.
2. **Global conservation status:** IUCN category followed by citation of South Africa (RSA), Botswana and/or Namibia, if endemic within the borders of any one, two or all three countries.
3. **Seasonal activity bar:** Qualitative assessment based on months in which collections or samples were taken.
4. **Map:** Distribution in southern Africa according to presence in 1/16th degree squares across a map panel extending from 17°S to 33°E (South Africa, Botswana, Namibia, most of Zimbabwe, extreme south of Mozambique); usually with an inset showing known or estimated range in Africa (Figure 2).
5. **Type localities:** One or more type localities quoted from original published descriptions of valid

species and their synonyms; current changes in locality names and/or qualifying notes are added where necessary.

6. **Taxonomy:** Species status is usually cited as 'Accepted species' although additional notes are provided if status is disputed or if there is appreciable intraspecific variation.

7. **Distribution:** A general description is provided for the species range as many taxa show distributions extending beyond the confines of the map (see **Map**).

8. **Locality data:** Ranges and mean values ± SD for altitude, annual rainfall and annual temperature are provided for each species. These data are derived from average values within 5 × 5 km polygons extracted from GIS base maps for all of southern Africa south of 15°S.

9. **Habitat:** Soil and vegetation associations in southern Africa are described according to available data, qualitative or quantitative, published or unpublished.

10. **Food types:** Food type associations in southern Africa are described according to available data, qualitative or quantitative, published or unpublished.

11. **Temporal activity:** Diel and seasonal periodicity in southern Africa are described according to available data, qualitative or quantitative, published or unpublished. If available, data describing short-term responses to weather conditions are also included.

12. **Ecoregions:** For species with distributions partly or entirely within Botswana and/or Namibia, citations are made for coincidence with the ecoregions of Olson et al. (2001). These citations include the ecoregions of Zimbabwe and the extreme south of Mozambique for species also occurring in those countries.

13. **Bioregions:** For species occurring partly or entirely within South Africa, citations are made for coincidence with the floral areas of Mucina & Rutherford (2006). For species with larger ranges citations are at biome and bioregion scale. For species with smaller ranges, citations are often also at vegetation unit scale.

14. **Assessment rationale:** An EOO (Extent of Occurrence) is provided for most species and a general discussion is made to support the allotted IUCN threat category. This may include notes on the sizes of the EOO and AOO (Area of Occupation) as well as generalisation versus specialisation to soil type, vegetation structure, and/or food type. Restricted range and occurrence of preferred soil types, increasing range restriction of mammals dropping preferred dung types or association with threatened vegetation types are particularly pertinent to the conservation status of dung beetles.

15. **Conservation measures:** Either 'None recommended' or a discussion of recommended measures derived from the **Assessment rationale** (pg. 12) section. Coincidence of each species with protected areas and a listing of a few of the more important reserves, if any.

Summary tables

Three summary tables (Appendices 1, 2 and 3) have been developed from information in the species accounts. Summary Table 1 (Appendix 1) is for species found in South Africa. This includes data on proportional distribution across the biomes of Mucina and Rutherford (2006) based on occurrence in 1/16th of a degree squares. It also includes IUCN categories and summarises putative ecological bias in each species if known. Summary Table 2 (Appendix 2) is for species recorded in Namibia and Botswana. It includes data on proportional distribution across the ecoregions of Olson et al. (2001) based on occurrence in 1/16th of a degree squares. It also lists IUCN categories for each species that is either restricted to those two countries or is also found in South Africa. The number of species found in each biome or ecoregion has been added at the base of each summary table. These numbers are dependent on climate and area of each region. There are some differences to the numbers defined for climatic regions reported above (see last paragraph under **Climatic associations**). Appendix 3 summarises climatic, altitudinal, distributional and range size data for each species included in the species accounts.

The numbers of species recorded for biomes do not clearly show the decline in species numbers from NE to SW. The low numbers shown for winter (62) and bimodal (86) rainfall regions (Davis 2002) are hidden as the Fynbos Biome combines the area of both regions although overall numbers are similar (130). Numbers of species recorded at localities may be a better criterion on which to base NE to SW declines. For instance, over one year, species assemblages at winter rainfall localities in the Western Cape (Cape Peninsula shrubland: 13; SW coast shrubland: 23–33), were much lower than those in the mid-summer rainfall region on the Gauteng bushveld (sandy clay loam, open woodland: 66; deep sand, open woodland: 76). In the Western Cape, highest temperatures coincide with the dry season so that activity peaks are in spring and autumn whereas activity peaks and highest temperatures both coincide with the rainy season on the Gauteng bushveld (Davis 2002, see pg. 11 under **Seasonal activity**).

Subfamily SCARABAEINAE

Latreille, 1802

The Scarabaeinae is one of 16 extant subfamilies constituting the diverse beetle family Scarabaeidae. In terms of numbers of species, the Scarabaeinae are primarily diversified to feed and breed using vertebrate dung although there are various African groups with different ecological specialisations, including carrion or fungus-feeding, or poorly known habits, in forest leaf litter.

Until recently, the subfamily has been divided into 12 tribes based on morphological characters (Smith 2006). However, both morphological and molecular phylogenies show that only nine are monophyletic (three not represented in Africa) whereas the remaining three are extensively polyphyletic (Philips et al. 2004; Monaghan et al. 2007). Although topology differs radically between different global molecular phylogenies (Monaghan et al. 2007; Gunter et al. 2016; Tarasov & Dimitrov 2016), the most recent study was used to propose a partial revision of tribal classification. This proposal retained eight of the old tribal units with unchanged membership (Gymnopleurini, Scarabaeini, Onitini, Onthophagini, Oniticellini, Phanaeini, Eucraniini, Eurysternini). Names of the other four were also retained but with expanded (Sisyphini) or radically reduced membership (Ateuchini, Canthonini/Deltochilini, Coprini) and the added suffix of *sensu novo* [new sense]. For those polyphyletic tribes with radically reduced membership, 100 genera were given the status of *incertae sedis* (uncertain placement) and the geographical range of two tribes was reduced to the Americas (Ateuchini, Canthonini/Deltochilini).

Revision of tribal classification is necessarily incomplete due to different sets of genera included in each molecular phylogenetic study and frequent differences between evolutionary relationships claimed for the same genera. Out of ~261 valid genera and ~6 293 valid species recorded worldwide, the phylogenies analyse relationships between only 38.3–52.5% of the genera and a very much smaller proportion of the species. Therefore, further analyses are required to support a full revision of tribal classification. Under these circumstances, we have retained the old 12 tribe classification system (see below) to arrange the species accounts in this book. However, we have modified the membership of the Coprini and Ateuchini (old sense) according to the morphological phylogeny of Montreuil (1998). In addition, we have treated the membership of the three polyphyletic tribes according to the molecular phylogeny of Tarasov & Dimitrov (2016) to better reflect evolutionary relationships.

Twelve tribes (Smith 2006)

Nine tribes recorded in southern Africa

Polyphyletic
Centred on southern continents (Neotropical, Afrotropical, Australasia) with limited northern presence

1. Ateuchini Perty, 1830 (in new sense only Americas; all other genera *incertae sedis*).
2. Canthonini van Lansberge, 1874a (= Deltochilini Lacordaire, 1856) (in new sense only Americas; all other genera *incertae sedis*; but see notes for Sisyphini below).

Afro-Eurasia, Americas and Australia

3. Coprini Leach, 1815 (in new sense only two genera in Afro-Eurasia and Americas; all other genera *incertae sedis*).

Monophyletic for the most part
Restricted to Afro-Eurasia (Afrotropical, Palaearctic, Oriental)

4. Gymnopleurini Lacordaire, 1856.
5. Onitini Castelnau, 1840.
6. Scarabaeini Latreille, 1802.

Centred in Afro-Eurasia, also variously in Americas and Australia

7. Oniticellini Kolbe, 1905 (also a few species in the Americas).
8. Onthophagini Burmeister, 1846 (*Onthophagus* species also widespread in the Americas and Australia).
9. Sisyphini Mulsant, 1842 (two species in central America; in new sense with addition of genus *Epirinus* Dejean, 1833 (formerly Canthonini), which is now removed to the revalidated tribe, Epirinini van Lansberge, 1874a (Daniel et al. 2020)).

Three tribes restricted to the Americas

Monophyletic for the most part

10. Phanaeini Hope, 1838 (Nearctic, Neotropical).
11. Eucraniini Burmeister, 1873 (only Neotropical).
12. Eurysternini Vulcano, Martinez & Pereira, 1961 (only Neotropical).

TRIBE ATEUCHINI

Perty, 1830

Subtribe Ateuchina Perty, 1830: As Ateuchidae; Type genus: *Ateuchus* Weber, 1801.

Synonyms:

= Choeridiidae Harold, 1867a; Type genus: *Choeridium* LePeletier & Serville, 1828 [= *Ateuchus* Weber, 1801, senior name].

= Demarziellini Balthasar, 1961a; Type genus: *Demarziella* Balthasar, 1961a [*incertae sedis*].

Subtribe Scatimina Vaz de Mello, 2008: Type genus: *Scatimus* Erichson, 1847a.

Smith (2006) and Bouchard et al. (2011) provide evidence for Ateuchini as the correct tribal name on the basis of precedence. Unlike Bouchard et al. (2011), we do not list the recent tribal names of Dichotomiini Perreira, 1954, and older Pinotinae Kolbe, 1905, as synonyms of the Ateuchini since their type genus (*Dichotomius* Hope, 1838 = *Pinotus* Erichson, 1847b), and other *Copris*-like genera, have been transferred to the tribe, Coprini, as supported by the morphological phylogeny of Montreuil (1998) (see tribal account for Coprini). However, nomenclature may change further following future revision (see below).

As defined by Montreuil (1998), the non-*Copris*-like membership of the tribe, Ateuchini, is represented globally within areas of tropical and warm temperate climate. In the old sense, 37 genera may be assigned to the tribe on morphological criteria (13 with morphological phylogenetic support). These occur in three biogeographical centres: Afrotropical/Oriental (7); Americas (mainly Neotropical: 29); Australia/New Guinea (1). However, molecular phylogenies show that this tribal membership is polyphyletic, comprising at least seven distantly related lineages for just 18.9% of the generic membership (Monaghan et al. 2007) or six lineages for 32.4% of the membership (Tarasov & Dimitrov 2016). As a result, Tarasov & Dimitrov (2016) redefine the Ateuchini as comprising three lineages restricted to the Americas. All other ateuchine genera are given the status of *incertae sedis*, including all those in Africa. Under these circumstances, we use the old classification system for the Ateuchini as defined by Montreuil (1998), pending a full revision of membership.

In the old sense, many ateuchine genera are forest endemics, including *Paraphytus* Harold, 1877a, in tropical Africa and the Oriental region. Other African genera include some forest or shade endemics plus grassland and savanna species. Most of the Afrotropical genera show some form of specialisation, one possibly kleptocoprid on other dung beetle species (*Pedaria* Castelnau, 1832), one constructing broods from material in rotten tree trunks (*Paraphytus*), three related genera possibly all primarily mycetophagous (*Coptorhina* Hope, 1833, *Delopleurus* Erichson, 1847b, *Frankenbergerius* Balthasar, 1938).

In the old sense, a total of six genera have been recorded for the Ateuchini in the Afrotropical region. Molecular (Monaghan et al. 2007) and morphological phylogenies (Montreuil 1998) suggest that these genera comprise three distinct lineages with those of *Pedaria* and *Paraphytus*, distant from that for the other four basally derived genera (*Sarophorus* Erichson, 1847b; *Delopleurus*; *Coptorhina*; *Frankenbergerius*). The recent partial revision of tribal classification (Tarasov & Dimitrov 2016) only partly supports these divisions with *Pedaria* in a separate lineage but *Paraphytus* classified together with the other four ateuchine genera in basal Scarabaeinae (Figure 5, pg. 699).

Two lineages are represented in Botswana, Namibia and/or South Africa where a total of five genera and possibly up to 37 species are found.

(1A) *Coptorhina* Hope, 1833: relatively species-poor genus with a southerly distributional bias including four species centred on savanna or upland grassland in southern Africa.

(1B) *Delopleurus* Erichson, 1847b: two or three southern African savanna species in a relatively species-poor genus that is widespread in the Afrotropical and Oriental regions.

(1C) *Frankenbergerius* Balthasar, 1938: comprises only seven species found in shrublands and forests along the entire seaboard of South Africa.

(1D) *Sarophorus* Erichson, 1847b: relatively species-poor genus with a southerly distributional bias including ten species centred on dense shrubland, forest or margins of upland grassland in southern Africa.

(2) *Pedaria* Castelnau, 1832: Possibly represented by up to 13 species in savannas and upland grasslands of southern Africa but species accounts are only provided for five validated taxa of this widespread and species-rich Afrotropical genus.

Genus *Coptorhina* Hope, 1833

Type species and designation: *Coptorhina africana* Hope, 1833, by subsequent designation (Janssens 1939a).
Synonyms: None.
Last review: Entire genus reviewed by Frolov et al. (2008).

The long-established genus, *Coptorhina* Hope, 1833, is currently reduced to seven valid species after the revision of Frolov et al. (2008) described one new species, but identified nine previous names as synonyms resulting from high intraspecific, morphological variability with body size. The genus is restricted to the Afrotropical region where it is represented from central and E equatorial regions southwards to southern Africa.

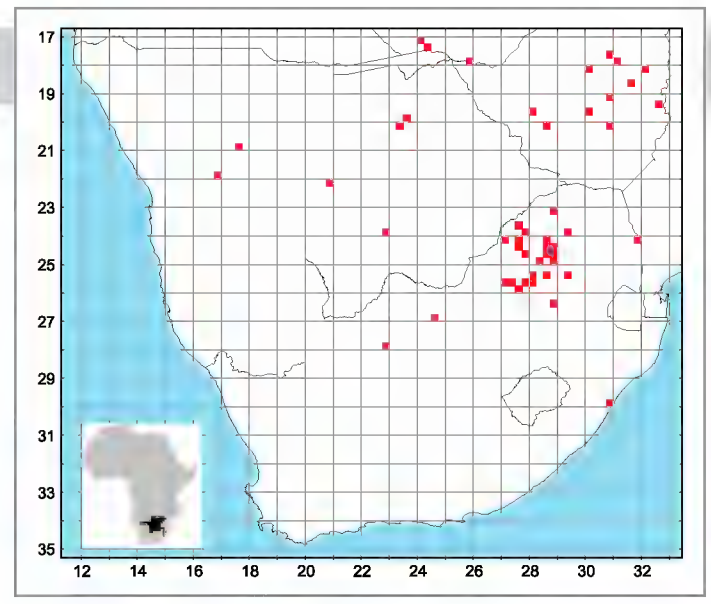
All species are macropterous comprising specialised mycetophages producing nests with a single brood pear of basidiomycete fragments lined with a clay shell (observed for *C. klugi* Hope, 1833; *C. auspicata* Péringuey, 1901).

Four species are found S of 15°S. Two show an E bias, one from E tropical savanna to Highveld Grassland and one restricted to drier Highveld Grassland. Two show an E savanna bias with additional scattered records in the drier centre and W of southern Africa. One of these is also distributed widely in the S and central African tropics.

Because of their widespread distributions and widely available food type, most species are assessed as Least Concern (LC) although one remains poorly known and Data Deficient (DD).

Coptorhina auspicata

Péringuey, 1901



No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'Transvaal (Rustenburg), Southern Rhodesia (Salisbury, Enkeldoorn), Ovampoland (Humbe)' [South Africa, Zimbabwe, Namibia], lectotype: 'Rhodesia. Enkeldorn. Darling.' [Chivhu in Zimbabwe].

Taxonomy: Accepted species; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.

Distribution: Frequently recorded in moist upland woody savanna with a widespread scatter of records elsewhere in the summer rainfall region of southern Africa; Zambia, Zimbabwe, Namibia, Botswana, South Africa.

Locality data (mean ± SD, range): Altitude: 1 139 ± 276, 165–1657 m; annual rainfall: 610 ± 138, 329–948 mm; annual temperature (max. + min. /2): 19.6 ± 1.6, 15.2–22.8°C (N=56).

Habitat: No quantitative assessment; limited DBRU collection records on sand (4), sandy loam (2) in grassland/pasture (3), shrub/woodland (3).

Food types: No quantitative assessment; limited DBRU collection records from dung of cattle (2), mushrooms (3), alighted on the soil surface (2).

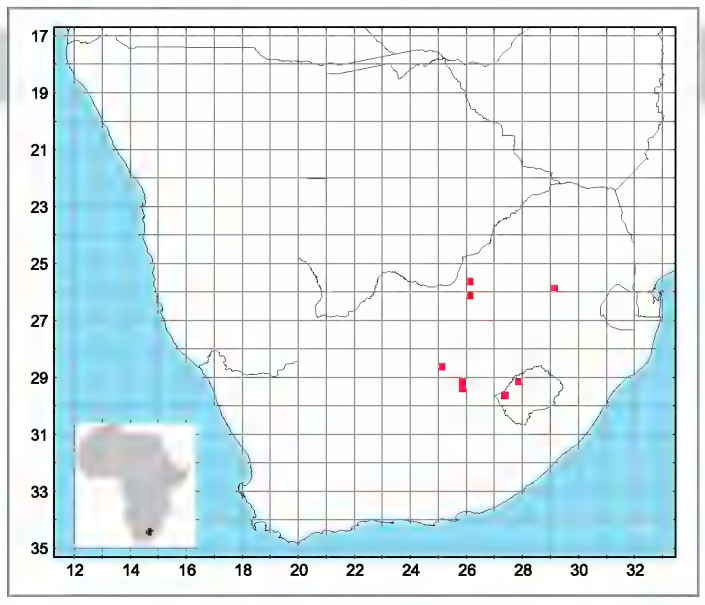
Temporal activity: Diurnal flight activity in the summer rainy season (Nov. to May); probably active under cooler conditions after rainfall owing to observed probable primary association with fungi; recorded in late afternoon (18:00) near Maun, Botswana.

Ecoregions Namibia, Botswana, Zimbabwe: Southern African Bushveld (AT0717), Southern Miombo Woodlands (AT0719), Zambezian Baikiaea Woodlands (AT0726), Xeric Kalahari Savanna (AT1309).

Bioregions South Africa: Primarily in Central Bushveld (SVcb) (Savanna Biome) with a few records in four other bioregions in the Savanna, Grassland and Indian Ocean Coastal Belt biomes.

Assessment rationale: EOO = 898 960 km^2; widespread EOO, but frequency of records apparently biased to moist savanna, which may be associated with food specialisation to fungi; poorly known ecologically, but possibly associated with sandy soils; assessment as Least Concern (LC) probably justified on the basis of widespread EOO and AOO.

Conservation measures: Assessment of conservation status would be improved by quantitative data on soil and vegetation associations as well as confirmation of specialist association with basidiomycete fungi; not widely protected, but recorded from several nature reserves including D'Nyala and Doorndraai (South Africa).



Coptorhina excavata

Frolov, Akhmetova & Scholtz, 2008

No synonyms

Global: DD
Endemic: RSA, Lesotho

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Mamathes Basutoland' [Lesotho].
Taxonomy: Accepted species; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.
Distribution: Dry to moist, NW Highveld Grassland, South Africa.
Locality data (mean ± SD, range): Altitude: 1 451 ± 146, 1 293–1 662 m; annual rainfall: 586 ± 121, 425–733 mm; annual temperature (max. + min. /2): 16.4 ± 1.2, 14.7–18.3°C (N=8).
Habitat: No quantitative assessment; one DBRU collection record on sandy loam in grassland.
Food types: No quantitative assessment; one DBRU collection record from a 'toadstool' (basidiomycete fungus).
Temporal activity: Diurnal flight activity in the summer rainy season (Oct. to Feb.); probably active under cooler conditions after rainfall owing to probable primary association with fungi.
Bioregions South Africa: Dry Highveld Grassland (Gh), W Mesic Highveld Grassland (Gm) (Grassland Biome).
Assessment rationale: EOO = 115 840 km^2; ecologically poorly known, but a single observation suggests a specialist mycetophage like other *Coptorhina* species; relatively low number of records probably related to its specialist behaviour; probably deserves a Least Concern (LC) assessment on basis of relatively large range, but currently assessed as Data Deficient (DD) since possible effects of widespread habitat transformation are unknown (Gh: 4–63%; Gm: 6–69%).
Conservation measures: To assess conservation status, quantitative data are required on ecological associations and effects, if any, of habitat transformation; protected in Telperion Nature Reserve (South Africa).

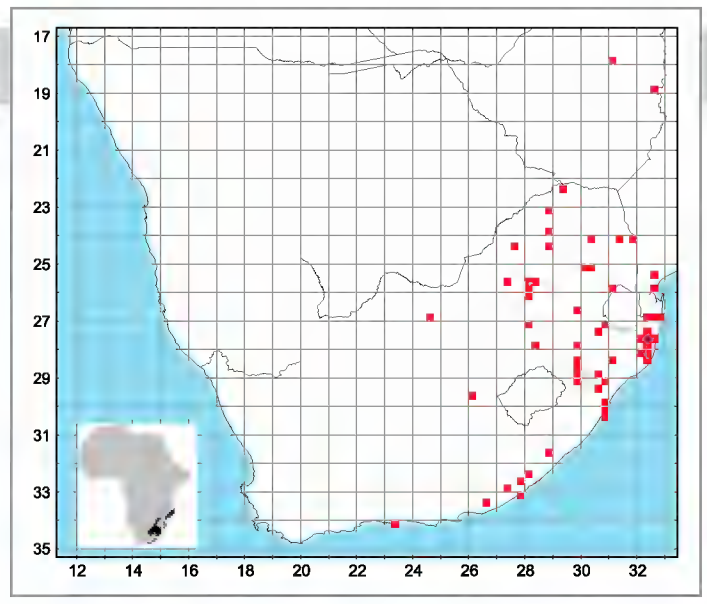
Coptorhina klugi

Hope, 1833

= *Coptorhina africana* Hope, 1833
= *Coptorhina obtusicornis* Boheman, 1857
= *Coptorhina vicina* Péringuey, 1901
= *Coptorhina optata* Péringuey, 1901
= *Coptorhina punctata* Ferreira, 1954a

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: *C. klugii*: 'Caput Bonae Spei' [Cape of Good Hope, South Africa]; *C. africana*: 'Sierra Leone' [?locality error]; *C. obtusicornis*: 'juxta fluvium Limpopo' [near Limpopo River, southern Africa]; *C. vicina*: 'Mozambique (Rikatla)' [Ricatla, S Mozambique]; *C. optata*: 'Southern Rhodesia (Manica)' [E Zimbabwe]; *C. punctata*: 'Transvaal : Pretoria' [Tshwane/Pretoria, Gauteng, South Africa].

Taxonomy: Accepted species cited as *Coptorhina klugii* Hope, 1835, by Frolov et al. (2008); original description of *C. klugii* Hope, 1833:97 is preceded by that of a synonym, *C. africana* Hope, 1833:96, whose cited type locality is far outside the known range of *C. klugi* and whose name is now modified to modern style; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.

Distribution: Primarily moist areas along SE African coastline, edge of E escarpment, N edge of Highveld, Waterberg and Blouberg with scattered records elsewhere: South Africa, Lesotho, Zimbabwe, Mozambique.

Locality data (mean ± SD, range): Altitude: 646 ± 584, 0–1 735 m; annual rainfall: 751 ± 142, 315–1 016 mm; annual temperature (max. + min. /2): 19.5 ± 2.6, 14.4–25.2°C (N=73).

Habitat: No quantitative assessment; limited DBRU collection records on deep sand (3), sandy clay loam (3) in upland grassland (2), open woodland (1), lowland woodland (3).

Food types: No quantitative assessment; limited DBRU collection records on dung of cattle (3) or basidiomycete mushrooms (2); also recorded to meat and banana bait.

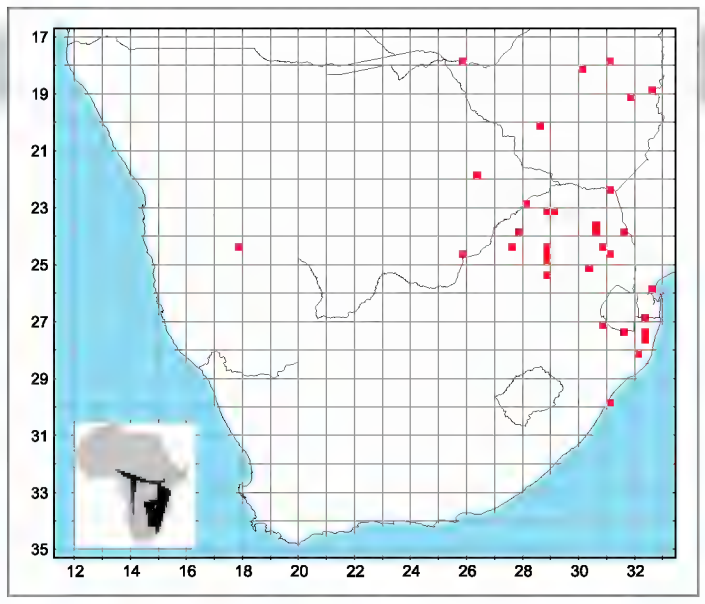
Temporal activity: Diurnal flight activity, primarily in the summer rainy season (Oct. to Apr.); probably active under cooler conditions after rainfall owing to probable primary association with fungi.

Ecoregions Zimbabwe, Mozambique: Southern Zanzibar-Inhambane Coastal Forest Mosaic (AT0128), Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Primarily Indian Ocean Coastal Belt Biome; E edge Sub-Escarpment Grassland (Gs), N and NE edges Mesic Highveld Grassland (Gm) (Grassland Biome); Waterberg area in Central Bushveld (SVcb), moist SE Lowveld (SVl) (Savanna Biome); scattered records in six other bioregions.

Assessment rationale: EOO = 681 450 km^2; in the laboratory, brood pear constructed from macerated mushroom fragments supports specialisation to mycetophagy; but, little support offered by published field data; habitat associations also unclear; assessed as Least Concern (LC) on basis of wide distribution, but limited ecological data suggests that Data Deficient (DD) would be more appropriate.

Conservation measures: Assessment of conservation status would be much improved by quantitative ecological data from both upland and coastal situations, including precise food association data and effects, if any, of soil type bias and habitat transformation; lowland populations protected in uMkhuze Game Reserve (South Africa).



Coptorhina nitidipennis

Boheman, 1857

= *Coptorhina bicolor* Ancey, 1883
= *Coptorhina seminitida* Fairmaire, 1893
= *Coptorhina subaenea* Janssens, 1939a
= *Coptorhina saganicola* Müller, 1947
= *Coptorhina pygmaea* Balthasar, 1963a

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *C. nitidipennis*: 'prope fluvium Gariep' [close to Orange River, South Africa]; *C. bicolor*: 'l'Usagara' [Usagara, NE Tanzania]; *C. seminitida*: 'Choa' [Shewa, Central Ethiopia]; *C. subaenea*: 'Congo belge : Élisabethville : Lubumbashi' [Democratic Republic of the Congo (DRC): Lubumbashi]; *C. saganicola*: Not stated; *C. pygmaea*: 'Kamerun: Joko' [Cameroon: Joko].

Taxonomy: Accepted species; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.

Distribution: Widespread, mostly in moist savanna from equatorial to southern Africa; Nigeria, Cameroon, Central African Republic, southern Sudan, Ethiopia, Democratic Republic of the Congo, Uganda, Kenya, Tanzania, Malawi, Zambia, Zimbabwe, Mozambique, Angola, Namibia, Botswana, South Africa.

Locality data (mean ± SD, range): Altitude: 837 ± 562, 0–1 627 m; annual rainfall: 722 ± 318, 181–1 170 mm; annual temperature (max. + min. /2): 20.3 ± 2.5, 14.7–24.9°C (N=39).

Habitat: No quantitative assessment; one DBRU collection record from sandy loam.

Food types: No quantitative assessment; one DBRU collection record: caught in flight.

Temporal activity: Diurnal flight activity in the summer rainy season (Nov. to Apr.); probably active under cooler conditions after rainfall owing to observed probable primary association with fungi.

Ecoregions Namibia, Botswana, Zimbabwe: Centred on Southern African Bushveld (AT0717), Southern Miombo Woodlands (AT0719); marginal in four other ecoregions.

Bioregions South Africa: Central Bushveld (SVcb), Lowveld (SVl), Mopane (SVmp) (Savanna Biome); marginal in one other bioregion.

Assessment rationale: EOO = 4 106 325 km^2 (gross estimate); assumed to be a specialist mycetophage like other *Coptorhina* species; assessed as Least Concern (LC) on basis of extremely large range although deserves Data Deficient (DD) status since it is very poorly known ecologically.

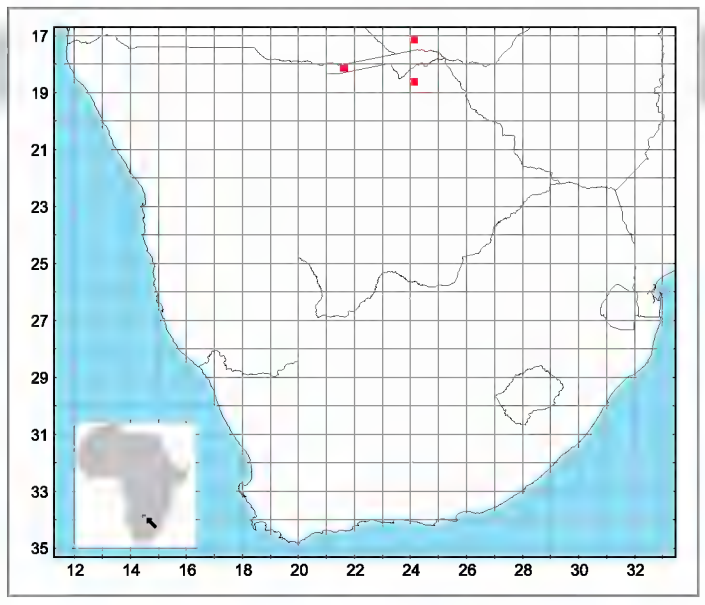
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, particularly possible effects of habitat transformation; protected in uMkhuze Game Reserve (South Africa).

Genus *Delopleurus* Erichson, 1847b

Type species and designation: *Delopleurus pullus* Boheman, 1857, by subsequent monotypy (Boheman 1857).
Synonyms: None.
Last review: Entire genus reviewed by Frolov (2014) with the addition of one new species (Král 2014).

The long-established genus, *Delopleurus* Erichson, 1847b, shows an Afro-Eurasian distribution pattern. It currently comprises ten valid species centred in the Afrotropical (7), W Oriental (India: 2) and extreme S Palaearctic (Yemen, Socotra: 1) regions. They are suspected to be mycetophagous, like *Coptorhina* species, but records from mushrooms, dung and carrion are too few to determine any specialisation.

Two, perhaps three species have been recorded S of 15°S. Two have been recorded from savanna in two or all three countries comprising South Africa, Botswana and Namibia. A single record for a third species represents an outlier occurrence far outside its main range in the tropics.



Delopleurus darrenmanni

Frolov, 2014

No synonyms

Global: DD

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Namibia W. Caprivi Park Nova, 5 km north of Okavango River 18°09'56' S, 21°44'31' E'.

Taxonomy: Accepted species.

Distribution: Known only from a small range on floodplains in central southern Africa: N Botswana, NE Namibia, SW Zambia.

Locality data (mean ± SD, range): Altitude: 907 ± 21, 889–930 m; annual rainfall: 609 ± 89, 541–710 mm; annual temperature (max. + min. /2): 22.3 ± 0.3, 22.1–22.6°C (N=3).

Habitat: No quantitative assessment; no data.

Food types: No quantitative assessment; holotype recorded on fungi.

Temporal activity: Probably diurnal flight activity in the summer rainy season (Nov., Dec.).

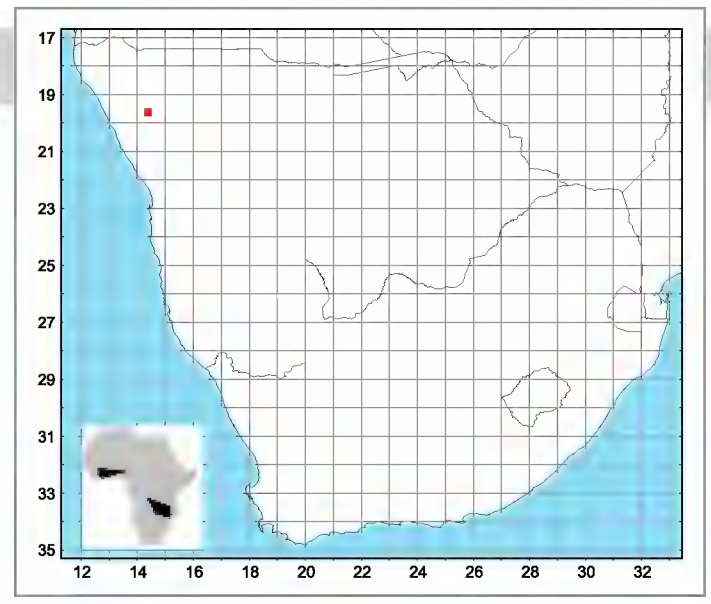
Ecoregions Namibia, Botswana: Centred on Zambezian Flooded Grasslands (AT0907) (two out of three records) (third record from floodplain at Savuti in Zambezian and Mopane Woodlands: AT0725).

Assessment rationale: EOO = 22 265 km^2 (presumably underestimated); probably a specialist mycetophage centred on moist floodplains that would be favourable for fungal growth; however, ecologically poorly known; in the absence of quantitative data, assessed as Data Deficient (DD).

Conservation measures: In order to determine conservation status, a quantitative survey is required to determine the full EOO, AOO and ecological associations; this needs to be centred on the Okavango, Kafue and Cuando (SW Angola) floodplains plus the edges of adjacent ecoregions; protected in Chobe National Park (Botswana) and West Caprivi Park (Namibia).

Delopleurus gilleti

Janssens, 1939a



No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'Togo; Congo belge : Kasai : forêt de Luebo....; Katanga : Lulua : rivière Kapelekese' [holotype: Togo; paratypes: Democratic Republic of the Congo (DRC)].

Taxonomy: Accepted species, but record from N Namibia (Frolov 2014) falls within the range of *D. pullus* Boheman, 1857, and represents an extreme outlier compared to remaining known localities for *D. gilleti* (see range map).

Distribution: Widespread intertropical distribution, primarily in W and SE African savanna either side of the rain forest belt; range may be truly disjunct or a collection artefact; Côte d'Ivoire, Mali, Togo, Nigeria, S Democratic Republic of the Congo (DRC), Tanzania, Malawi, Zambia, Mozambique, Namibia.

Locality data (mean ± SD, range): Altitude: 791 ± 401, 329–1 046 m; annual rainfall: 678 ± 379, 243–933 mm; annual temperature (max. + min. /2): 21.0 ± 3.4, 17.5–24.3°C (N=3).

Habitat: No quantitative assessment; one DBRU collection record from gravelly sandy loam in a fallow field (Nigeria), but paratype material recorded from tropical forest.

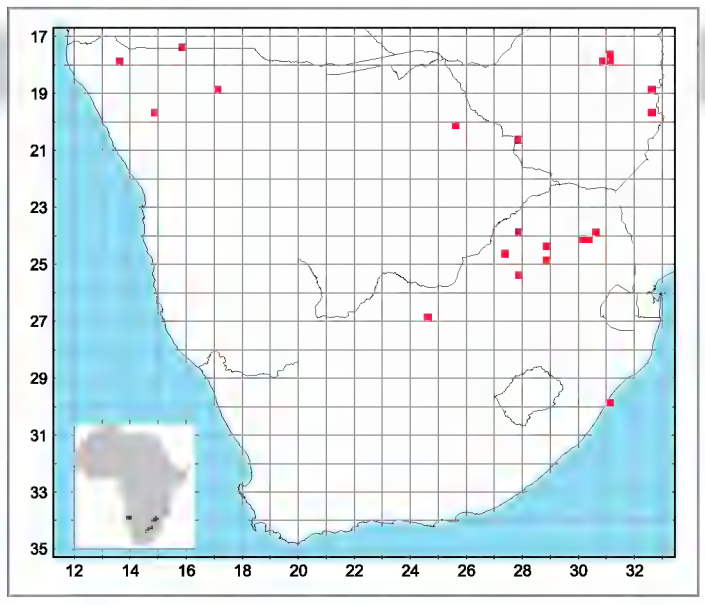
Food types: No quantitative assessment; limited DBRU collection records from mushroom (14 individuals) and cattle dung (1 individual).

Temporal activity: Probably diurnal flight activity in the summer rainy season (Jan., Feb.).

Ecoregions Namibia: Namibian Savanna Woodlands (AT1316).

Assessment rationale: EOO = 1 773 210 km^2 (range without Namibian record); marginal occurrence in N southern Africa; assessed as Least Concern (LC) on basis of extremely widespread EOO, and, as a probable specialist mycetophage, apparent occupation of a wide range of vegetation types, including disturbed agricultural lands.

Conservation measures: Assessment of conservation status would be improved by further validation of the Namibian record and quantitative data on EOO, AOO and ecological associations; not currently known from protected areas in southern Africa.



Delopleurus pullus

Boheman, 1857

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'prope fluvium Limpopo' [close to Limpopo River, southern Africa], lectotype: 'Caffraria' [inexact, southern Africa].

Taxonomy: Accepted species.

Distribution: Widespread in southern African dry to moist savanna; disjunct pattern may be a collecting artefact; South Africa, Botswana, Namibia, Angola, Zimbabwe, Malawi, Mozambique.

Locality data (mean ± SD, range): Altitude: 1 063 ± 352, 1–1 550 m; annual rainfall: 701 ± 263, 311–1 515 mm; annual temperature (max. + min. /2): 19.7 ± 1.7, 17.1–22.9°C (N=23).

Habitat: No quantitative assessment; no data.

Food types: No quantitative assessment; one series of five individuals recorded from a basidiomycete mushroom at Legonyane, North West Province, South Africa.

Temporal activity: Diurnal flight activity in the summer rainy season (Nov. to Feb.).

Ecoregions Namibia, Botswana, Zimbabwe: Southern African Bushveld (AT0717), Southern Miombo Woodlands (AT0819), Angolan Mopane Woodlands (AT0702), Namibian Savanna Woodlands (AT1316).

Bioregions South Africa: Centred on Central Bushveld (SVcb) with marginal records in Lowveld (SVl) and Eastern Kalahari Bushveld (SVk) (Savanna Biome).

Assessment rationale: EOO = 186 855 km² (underestimated); probable specialist mycetophagous habits result in limited records and apparent disjunct distribution; although poorly known ecologically, assessed as Least Concern (LC) on the basis of wide EOO.

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, particularly confirmation of mycetophagous habits and effects of habitat transformation, if any; protected in several South African nature reserves: D'Nyala, Ben Alberts.

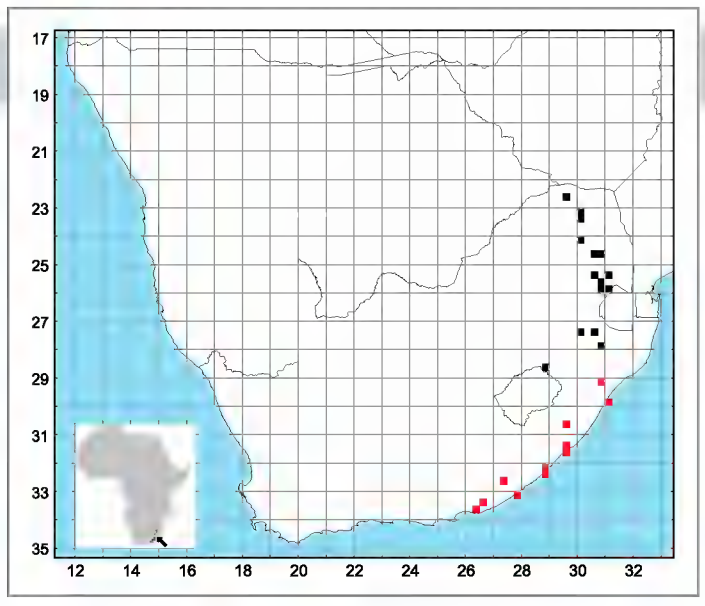
Genus *Frankenbergerius* Balthasar, 1938

Type species and designation: *Frankenbergerius mirabilis* Balthasar, 1938, by monotypy.
Synonyms: = *Pseudocoptorhina* Ferreira, 1954a: Type species: *Coptorhina armata* Boheman, 1857, by original designation.
Last review: Entire genus reviewed by Frolov & Scholtz (2005).

Frankenbergerius Balthasar, 1938, is endemic to the W, S and E seaboards plus NE edge of the Highveld, South Africa. It is currently represented by seven species. One widespread, forest taxon occurs as two subspecies centred on the SE coast or NE escarpment and is assessed as Least Concern (LC). Records for the remaining six species are severely limited resulting in assessments of Data Deficient (DD).

Of the six poorly known species, three are centred in the summer rainfall region, primarily in forest, occurring variously on the SE coast and/or NE escarpment. The other three are centred in the Western Cape winter rainfall region on the SW or W coasts, possibly in shrubland. The two species centred in the highly transformed SW Cape may deserve threat categories.

Ecological habits are unclear as records of food type are limited in number and have been made, sporadically, on fungi, fruit and dung.



Frankenbergerius armatus

(Boheman, 1857)

ssp. *armatus* (Boheman, 1857)
= *Coptorhina granulifera* Harold, 1871a
= *Frankenbergerius mirabilis* Balthasar, 1938
ssp. *tuberculatus* Frolov & Scholtz, 2005

Global: LC (see IUCN Red List – LC)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: ssp ***armatus*** as *Epirhinus armatus*: 'Caffraria tota' [inexact, southern Africa], lectotype: 'Caffraria'; *C. granulifera*: 'Port Natal' [Durban, South Africa]; *F. mirabilis*: 'Columbien, Chiriguana' [Colombia, S America; presumably an error, = mislabeled material]; ssp ***tuberculatus*** first of 13 listed type localities: 'Entabeni Forest Station [23°00'S, 30°14'E]' [Limpopo Province, South Africa].

Taxonomy: Accepted species; sexually dimorphic (head), characters vary in prominence with body size; divided into two subspecies although the differences are subtle.

Distribution: E South African endemic; SE coast and escarpment (subsp. *armatus*: red squares); NE escarpment (subsp. *tuberculatus*: black squares); citation from Angola is an error.

Locality data (mean ± SD, range): subsp. *armatus*: Altitude: 376 ± 429, 12–1 406 m; annual rainfall: 778 ± 178, 618–2 522 mm; annual temperature (max. + min. /2): 18.0 ± 1.9, 13.5–20.8°C (N=14); subsp. *tuberculatus*: Altitude: 1 216 ± 493, 19–1 635 m; annual rainfall: 839 ± 171, 381–1 157 mm; annual temperature (max. + min. /2): 17.3 ± 3.2, 8.7–22.0°C (N=17).

Habitat: No quantitative assessment; no soil type data, however, 37% of available records (13 out of 35) cited from forest, three from high altitude grassland (remainder not stated); a number of records from litter of indigenous and plantation forest (*Pinus*, *Quercus*, *Eucalyptus*).

Food types: No quantitative assessment; recorded from mushrooms, fungous tree bark and trunks, rotten *Cussonia* fruit; also sampled to banana bait.

Temporal activity: Not known, but presumably shows diurnal flight activity, primarily in the summer rainy season (Oct. to May).

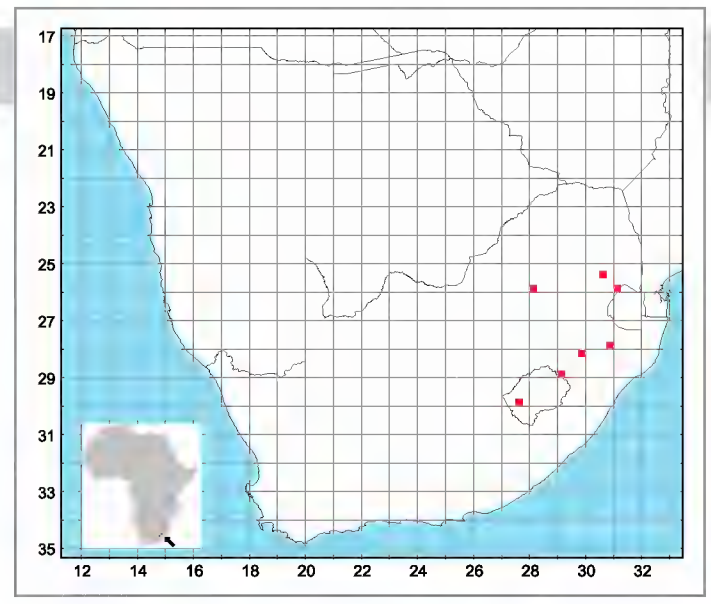
Bioregions South Africa: Although some records map onto bushveld, forest and thicket vegetation units, they do not clearly define habitat associations; in general, N records follow edge of E escarpment and Soutpansberg, representing edges of the Savanna (SV) and Grassland Biomes (G) (Lower = Lowveld (SVl), Mopane (SVmp), Sub-Escarpment Grassland (Gs); Upper = Mesic Highveld Grassland (Gm)); S records follow coast and edge of SE escarpment (Lower = Indian Ocean Coastal Belt Biome (CB), Albany Thicket Biome (AT); Upper = Sub-Escarpment Grassland (Gs) of the Grassland Biome; all separated by Sub-Escarpment Savanna (SVs)).

Assessment rationale: EOO = 65 575 km^2; widely distributed along SE coast and E escarpment, but no clear assessment of habitat and food in the absence of quantitative data; however, shade vegetation dominates stated habitats and population density may be negatively influenced by its clearance; only fungi and fruit recorded as food types; currently assessed as Least Concern (LC) owing to large size of range, however AOO would be much smaller and liable to threat if primarily a shade specialist.

Conservation measures: Although currently cited as Least Concern (LC), quantitative ecological data are essential to adequately assess conservation status; protected in various South African forest reserves including Alexandra (part of Addo Elephant National Park), Dwesa-Cwebe Nature Reserve, Entabeni State Forest.

Frankenbergerius barratti

(Waterhouse, 1876)

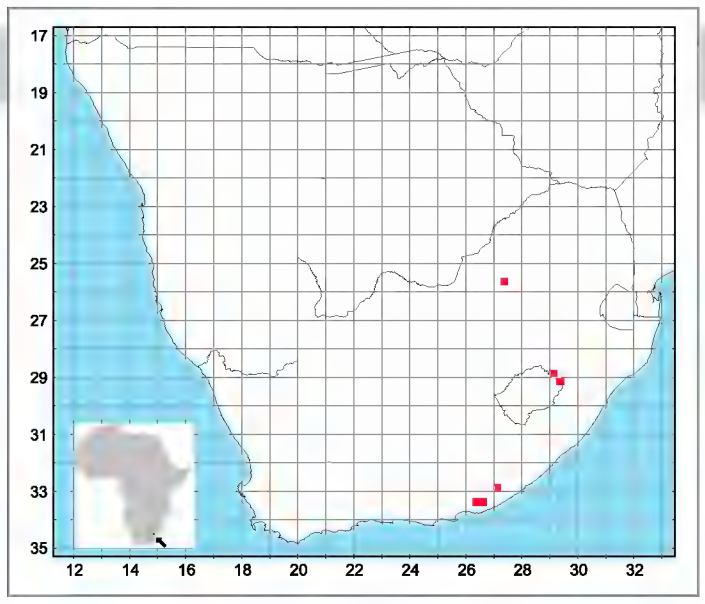


No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Coptorhina barratti*: 'S. Africa (Transvaal)' [South Africa].
Taxonomy: Accepted species; sexually dimorphic (head), characters vary in prominence with body size.
Distribution: Primarily follows moist climate along the N and E edges of the Highveld, South Africa and the W side of Lesotho.
Locality data (mean ± SD, range): Altitude: 1 320 ± 329, 699–1 800 m; annual rainfall: 768 ± 62, 698–855 mm; annual temperature (max. + min. /2): 16.3 ± 2.5, 12.0–20.3°C (N=8).
Habitat: No quantitative assessment; single records from both indigenous forest and natural Highveld Grassland on sandy clay loam.
Food types: No quantitative assessment; one individual sampled to pig dung, but food association essentially unknown.
Temporal activity: Not known, but presumably shows diurnal flight activity in the summer rainy season (Dec. to Mar.).
Bioregions South Africa: Within or close to the N and E edges of Mesic Highveld Grassland (Gm) (Grassland Biome).
Assessment rationale: EOO = 16 485 km^2; EOO based on spot records that all lie along the edge of Mesic Highveld Grassland suggesting a range that is < 20 000 km^2; *F. barratti* is represented by few museum specimens and is ecologically poorly known; apparent rarity may be real or a collection artefact; it may deserve an IUCN threat category of Vulnerable (VU), but is currently assessed as Data Deficient (DD).
Conservation measures: Quantitative ecological data is required to adequately assess conservation status in both natural highland grassland and forest patches in kloofs along the edge of the N Highveld; *F. barratti* could equally be under threat or rarely collected owing to specialised habits; not currently known from any officially protected area.



Frankenbergerius forcipatus

(Harold, 1880)

= *Coptorhina imitativa* Péringuey, 1901
= *Pseudocoptorhina forcipata* Ferreira, 1954a

Global: DD (see IUCN Red List – DD)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Coptorhina forcipata*: 'Cap bon. spei.' [Cape of Good Hope, South Africa; presumably inexact]; *C. imitativa*: 'Transvaal (Lydenburg)' [Mashishing, Mpumalanga, South Africa]; *P. forcipata*: 'Colónia do Cabo' ['Cape Colony', possibly Eastern Cape, South Africa].

Taxonomy: Accepted species; sexually dimorphic (head), characters vary in prominence with body size.

Distribution: South African endemic; scattered records along the Eastern Cape and KwaZulu-Natal escarpment; also Magaliesberg on the N edge of the Highveld.

Locality data (mean ± SD, range): Altitude: 1 220 ± 721, 443–2 403 m; annual rainfall: 662 ± 98, 531–819 mm; annual temperature (max. + min. /2): 15.2 ± 3.2, 9.7–19.2°C (N=6).

Habitat: No quantitative assessment; two of six available records cited as forest; no soil type data.

Food types: No quantitative assessment; recorded in small numbers in pitfall traps.

Temporal activity: Not known, but presumably shows diurnal flight activity in the summer rainy season (Dec. to Mar.).

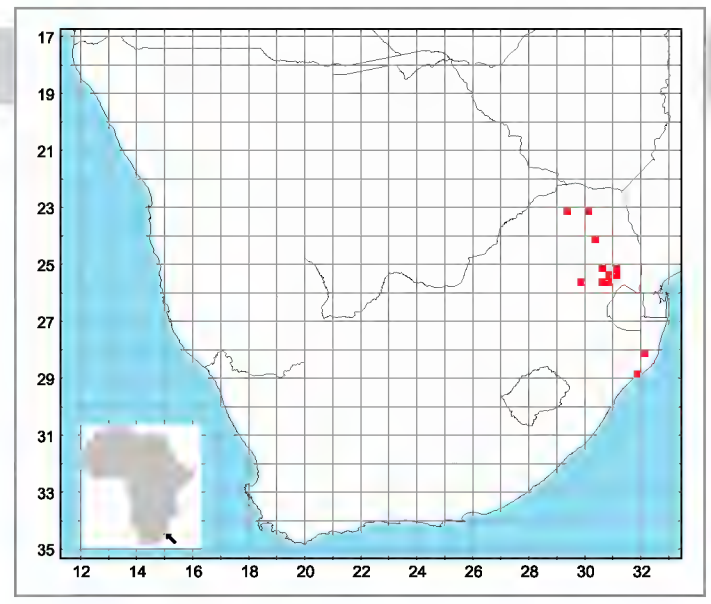
Bioregions South Africa: Possibly shaded patches in Central Bushveld (Moot Plains Bushveld (SVcb 8), Sub-Escarpment Savanna (Bhisho Thornveld (SVs 7)) (Savanna Biome); Forest Biome: Southern Mistbelt Forest (FOz 3), Northern Afromontane Forest (FOz 2) locality cited as forest, but does not map onto nearest patch within Drakensberg Grassland Bioregion (Gd) (Grassland Biome).

Assessment rationale: EOO = 21 625 km^2; ecologically extremely poorly known; limited records suggest possible forest or shade associations, but quantitative support required; large range, but AOO would be much smaller if it is a habitat specialist; currently assessed as Data Deficient (DD).

Conservation measures: A survey is required to accurately determine the EOO; quantitative ecological data is also required to assess the AOO and conservation status; protected in the uKhahlamba Drakensberg Park (World Heritage Site).

Frankenbergerius gomesi

(Ferreira, 1954a)



No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Pseudocoptorhina gomesi*: 'Uitzicht, Zoutpansberg' [Farm Uitzicht, W Soutpansberg, Limpopo Province, South Africa].

Taxonomy: Accepted species; sexually dimorphic (head), characters vary in prominence with body size.

Distribution: Records scattered along the W–E trending Soutpansberg, NE escarpment edge (Limpopo and Mpumalanga provinces), and the NE coast of KwaZulu-Natal, South Africa.

Locality data (mean ± SD, range): Altitude: 943 ± 488, 19–1 635 m; annual rainfall: 805 ± 98, 604–985 mm; annual temperature (max. + min. /2): 18.5 ± 2.1, 14.7–22.6°C (N=13).

Habitat: No quantitative assessment; limited records from riverine bush, eucalypt plantation, forest litter or pitfall traps in Roodewal Forest, Soutpansberg.

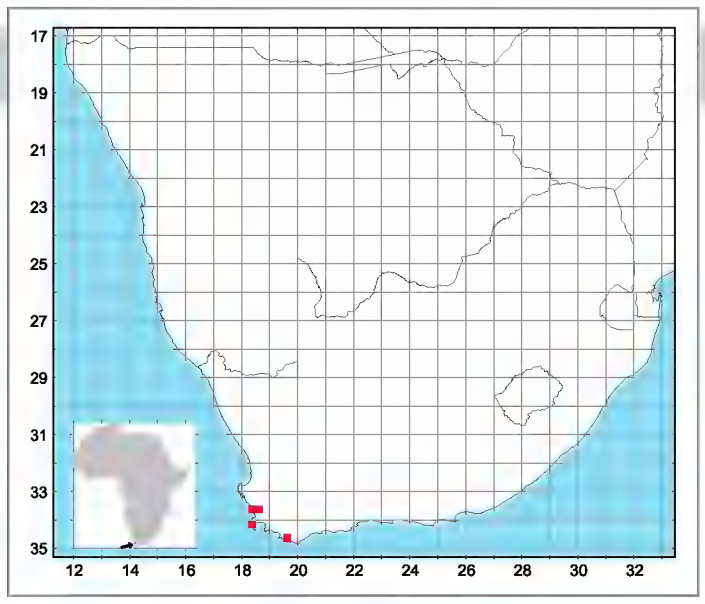
Food types: No quantitative assessment; limited records from fungus and fungous [tree] trunk; also sampled to pig dung baits.

Temporal activity: Not known, but presumably shows diurnal flight activity in the summer rainy season (Oct. to Feb.).

Bioregions South Africa: Records straddle the edges of the Grassland (G) / Savanna (SV) / Indian Ocean Coastal Belt Biomes (CB); only three map records close to or coinciding with Northern Mistbelt Forest (FOz 4) or Scarp Forest (FOz 5) patches [does not include samples from Roodewal Forest (Soutpansberg)]; in N: mapped non-forest records fall within Legogote Sour Bushveld (SVl 9), Sekhukune Montane Grassland (Gm 19), Soutpansberg Mountain Bushveld (SVcb 21) vegetation units.

Assessment rationale: EOO = 18 695 km^2; ecologically poorly known; limited records suggest a shade specialist that could be either a food type specialist or generalist; mapping unreliable for determining habitat associations, but, as a shade specialist, AOO would be much smaller than EOO and population density would be susceptible to clearance of woody vegetation; possibly deserves an IUCN threat category of Vulnerable (VU) on the basis of EOO <20 000 km^2 and probable disjunct AOO in small patches of shade vegetation; however, currently assessed as Data Deficient (DD).

Conservation measures: Quantitative ecological data is required to adequately assess conservation status; protected in Nelspruit and Lekgalameetse nature reserves.



Frankenbergerius nanus

(Péringuey, 1888)

No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Coptorhina nana*: 'near Constantia, Cape Colony' [near Constantia, Cape Town, Western Cape, South Africa].

Taxonomy: Accepted species, but very close to *F. opacus* Frolov & Scholtz, 2005; little sexual dimorphism noted.

Distribution: Small coastal range in the SW Western Cape, South Africa.

Locality data (mean ± SD, range): Altitude: 339 ± 374, 20–777 m; annual rainfall: 436 ± 87, 347–555 mm; annual temperature (max. + min. /2): 15.1 ± 1.8, 12.6–16.6°C (N=4).

Habitat: No quantitative assessment; three known localities from areas comprising deep sand or sandy loam where the natural vegetation is shrubland; one specimen sampled on deep sand in strandveld.

Food types: No quantitative assessment; one specimen sampled to cattle dung, but probably a chance record.

Temporal activity: Not known, but presumably shows diurnal flight activity; recorded during winter and spring in the winter rainy season (June to Sept.).

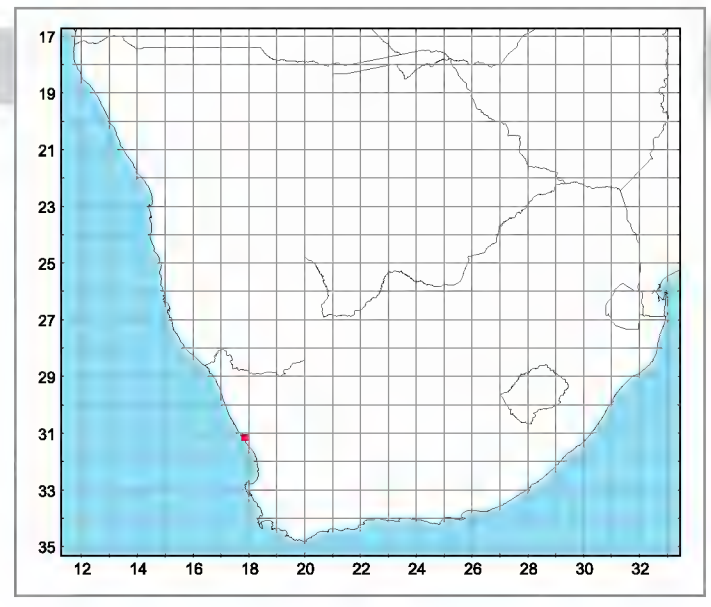
Bioregions South Africa: Vegetation units: Atlantis Sand Fynbos (FFd 4), Cape Flats Dune Strandveld (FS 6), Overberg Dune Strandveld (FS7) and Peninsula Granite Fynbos (FFg 3) (Fynbos Biome).

Assessment rationale: EOO = 2 995 km^2; little ecological data; assessed as Data Deficient (DD), but may deserve IUCN threat status approaching Endangered (EN) on basis of small range, low number of locations (3) and extensive transformation by urbanisation and arable farming in parts of its range (FFd 4: 40%; FS 6: 40%; FS 7: 5%; FFg 3: 56%).

Conservation measures: A survey is required to establish the full EOO and AOO to adequately assess conservation status; this survey should be combined with the collection of quantitative ecological data, particularly testing response to clearance of natural shrubland; not currently known to occur in any protected area although recorded at Pella Mission close to Pella Nature Reserve.

Frankenbergerius nitidus

Frolov & Scholtz, 2005

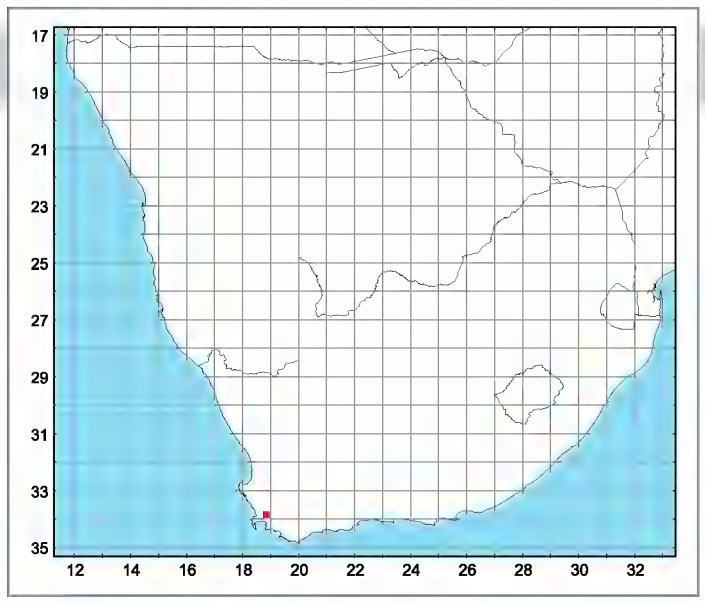


No synonyms

Global: DD (see IUCN Red List – DD)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'RSA, Northern Cape Province, Hoekbaai, 31°11'S, 17°47'E' [South Africa].
Taxonomy: Accepted species.
Distribution: Known only by a single female from the Namaqualand type locality on the arid W coast of South Africa.
Locality data (average): Altitude: 1 m; annual rainfall: 140 mm; annual temperature (max. + min. /2): 18.2°C (N=1).
Habitat: No quantitative assessment; known only from a vegetation unit comprising deep sand and open scrub / shrubland.
Food types: No quantitative assessment; a single, probable chance record from a white flower (Mesembryanthemaceae); food associations essentially unknown.
Temporal activity: Not known, but presumably shows diurnal flight activity; recorded during spring in the winter rainy season (Aug.).
Bioregions South Africa: Possibly Namaqualand Seashore Vegetation (Azonal: AZd 2) in which *Mesembryanthemum guerichianum* is listed as an important element, unlike adjoining inland Namaqualand Strandveld (SKs 7) (Succulent Karoo Biome).
Assessment rationale: EOO/AOO unknown; the range could be small and restricted to the coastline or wider; also ecologically extremely poorly known; possible threats impossible to assess although, at present, the area around the type locality appears little transformed, except at Hoekbaai itself; under these circumstances, assessed as Data Deficient (DD).
Conservation measures: A survey along the coastline and inland is required to determine the EOO and AOO to adequately assess conservation status; this survey should be combined with the collection of quantitative ecological data; not currently known to occur in any protected area.



Frankenbergerius opacus

Frolov & Scholtz, 2005

No synonyms

Global: DD (see IUCN Red List – DD)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Stellenbosch' [Western Cape, South Africa].
Taxonomy: Accepted species, but very close to *F. nanus* (Péringuey, 1888); little sexual dimorphism noted.
Distribution: Known only by seven individuals, all but one from the type locality in the SW Western Cape.
Locality data (average): Altitude: 228 m; annual rainfall: 435 mm; annual temperature (max. + min. /2): 16.9°C (N=1).
Habitat: No quantitative assessment; known only from an area comprising finer-grained soils in which the natural vegetation is Renosterveld shrubland.
Food types: No quantitative assessment; food associations unknown.
Temporal activity: Not known, but presumably shows diurnal flight activity; recorded in autumn during the winter rainy season (May).
Bioregions South Africa: Depending on accuracy of map coordinates, occupied vegetation units could be Swartland Shale Renosterveld (FRs 9) with clay loam soils (at Stellenbosch) or nearby Swartland Granite Renosterveld (FRg 2) with sandy loam soils (Fynbos Biome).
Assessment rationale: EOO/AOO unknown; no ecological data available; high levels of habitat transformation for arable farming or urbanisation around the single known locality (FRs 9: 90%; FRg 2: 80%); assessed as Data Deficient (DD), but probably deserves an IUCN threat category approaching Critically Endangered (CR) on the basis of few known museum specimens, no records since 1949, and their known occurrence at a single location in a highly transformed area.
Conservation measures: A survey is required to determine the EOO and AOO to adequately assess conservation status; this survey should be combined with the collection of quantitative ecological data, particularly to determine if its population density is influenced by clearance of natural shrubland; not currently known to occur in any protected area.

Genus *Pedaria* Castelnau, 1832

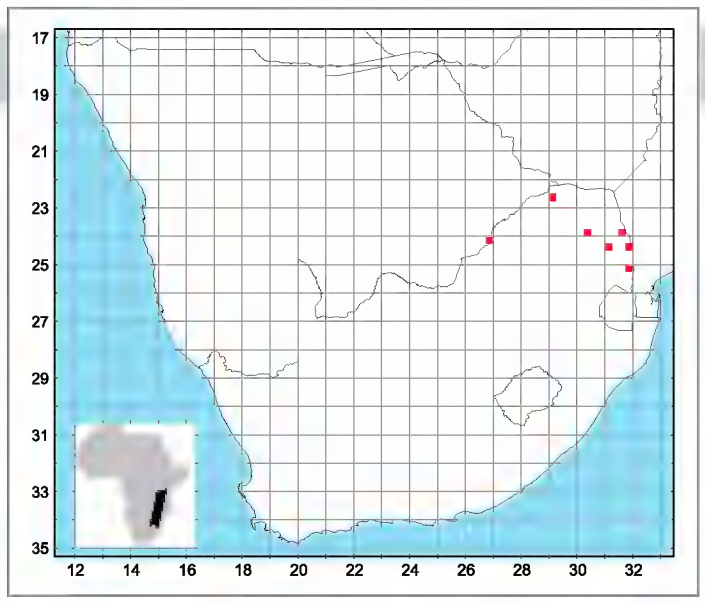
Type species and designation: *Pedaria nigra* Castelnau, 1832, by monotypy.
Synonyms: None.
Last review: Entire genus reviewed by Boucomont (1922); new species added, subsequently, by Balthasar (1937, 1939a, 1963b), Janssens (1939a), Ferreira (1962a), Cambefort (1982), Paulian et al. (1982); partial revisions and 27 new species added by Josso & Prévost (2003: 19; 2006a: 4; 2009a: 4).

The long-established genus, *Pedaria* Castelnau, 1832, currently comprises 60 species restricted to Afrotropical forests, savannas and grasslands, where they show kleptocoprid habits in association with dung buried by large tunnelling Scarabaeinae, especially *Heliocopris* (Cambefort 1991). The species are often difficult to separate without extraction of genitalia as external morphological differences are subtle. Illustrations of aedeagi are only provided for the new species recently described by Josso & Prévost (2003, 2006a, 2009a).

Except for one new species, the known southern African taxa were described long ago. Therefore, illustrations of aedeagi are lacking as in the revision of Boucomont (1922), which also seems to have missed the South African species, *Pedaria conformis* Péringuey, 1901. Of the eight described species recorded in South Africa, Namibia and/or Botswana, species accounts are provided for five more-or-less validated taxa. The remaining three taxa described from South Africa (*P. conformis* Péringuey, 1901; *P. aspera* Péringuey, 1901; *P. alternans* Waterhouse, 1890) may or may not be included in a further eight species that have now been recognised from collections made in this region.

The distribution patterns shown by *Pedaria* species in southern Africa are not fully represented by the five species for which species accounts are provided. These species show widespread or restricted savanna distributions with one centred along the E seaboard of Africa. However, two of the unnamed or unvalidated species show Kalahari or Highveld centred distributions, respectively.

Despite the poor state of knowledge of conservation status for *Pedaria*, it is probable that none of the 13 southern African species currently faces threats. Poor state of knowledge probably results partly from infrequent collection due to cryptic appearance in dung as well as the subtle taxonomic differences that complicate identification of species.



Pedaria barrei

Josso & Prévost, 2006a

No synonyms

Global: DD

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'East Kenya, Tsavo East, Voi Lodge' [Tsavo East National Park, Kenya].

Taxonomy: Accepted species; very close in appearance to *P. cylindrica* Fahraeus, 1857, but aedeagus quite different; four South African localities supported by extraction of aedeagi, three cited by Josso & Prévost (2006a).

Distribution: Mostly dry lowland savanna from S to E Africa: South Africa, Tanzania, Kenya.

Locality data (mean ± SD, range): Altitude: 496 ± 285, 153–878 m; annual rainfall: 560 ± 106, 403–710 mm; annual temperature (max. + min. /2): 21.8 ± 1.0, 20.8–23.1°C (N=7).

Habitat: No quantitative assessment; limited DBRU collection records: sand (1), sandy loam (1) in open shrub / woodland (2).

Food types: No quantitative assessment; limited DBRU collection records from dung of cattle (2), buffalo (1).

Temporal activity: Flight activity in darkness during the summer rainy season (Oct. to Mar.); attracted to light.

Bioregions South Africa: Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 1 460 055 km^2 (gross estimate); widespread, but difficult to assess conservation status as quantitative habitat and food association data are unavailable; records from elephant (2) and zebra dung (1) in Kenya are insufficient to support any bias to monogastric herbivore dung given southern Africa records from ruminant herbivore dung; assessed as Data Deficient (DD).

Conservation measures: Quantitative ecological data are required to adequately assess conservation status; protected in Kruger National Park (South Africa), Tsavo East National Park (Kenya).

Pedaria brancoi

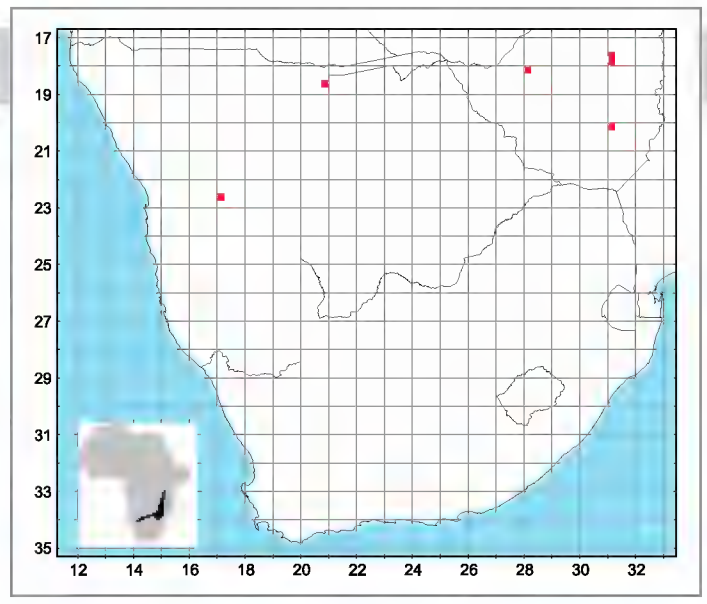
Josso & Prévost, 2003

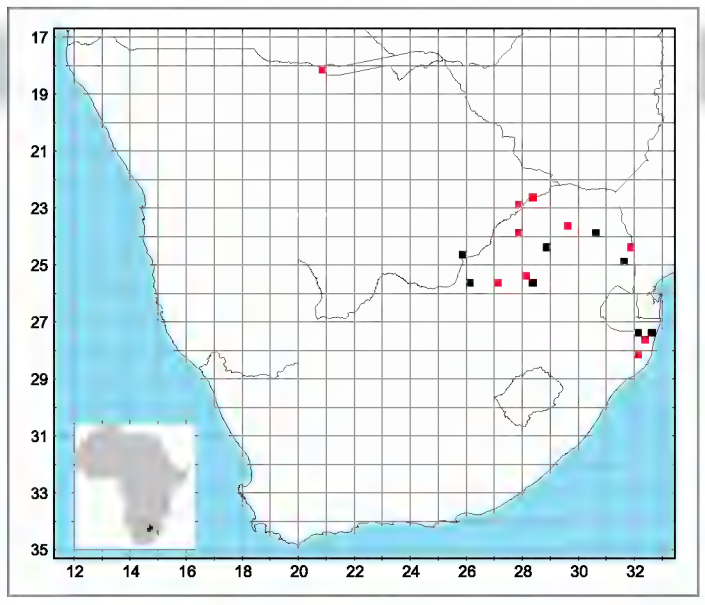
No synonyms

Global: DD

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Mozambique, Parc de Gorongoza' [Gorongosa National Park, central Mozambique].
Taxonomy: Accepted species.
Distribution: Lowland to upland, moist to dry savanna in S Central and SE Africa: Namibia, Zimbabwe, Mozambique, Tanzania.
Locality data (mean ± SD, range): Altitude: 1 087 ± 528, 59–1 818 m; annual rainfall: 729 ± 235, 354–1 136 mm; annual temperature (max. + min. /2): 20.9 ± 2.5, 18.3–25.2°C (N=8).
Habitat: No quantitative assessment; no data.
Food types: No quantitative assessment; no data.
Temporal activity: Flight activity in darkness, primarily during the summer rainy season (Nov. to Jan.; also June); attracted to light.
Ecoregions Namibia, Zimbabwe: N Zambezian and Mopane Woodlands (AT0725), Southern Miombo Woodlands (AT0719), Zambezian Baikiaea Woodlands (AT0726), Kalahari Acacia-Baikiaea Woodlands (AT0709), NW Kalahari Xeric Woodlands (AT1309).
Assessment rationale: EOO = 809 330 km^2 (gross estimate); widespread, but difficult to assess conservation status in absence of ecological data; assessed as Data Deficient (DD).
Conservation measures: Quantitative data on ecological associations is required before conservation status may be assessed; protected in Gorongosa National Park (Mozambique), Serengeti National Park (Tanzania).





Pedaria cylindrica

Fahraeus, 1857

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'prope fluvium Gariep' [near Orange River, South Africa].

Taxonomy: Accepted species; very close in appearance to *P. barrei* Josso & Prévost, 2006, but aedeagus quite different; out of 18 map localities, ten are supported by extraction of aedeagi (red squares).

Distribution: Moist southern African savanna: Namibia, Botswana, South Africa; also cited from Angola, Zimbabwe, Mozambique.

Locality data (mean ± SD, range): Altitude: 810 ± 457, 45–1 378 m; annual rainfall: 612 ± 130, 306–900 mm; annual temperature (max. + min. /2): 20.3 ± 1.7, 18.1–22.6°C (N=22).

Habitat: No quantitative assessment; DBRU collection records: sand (2), sandy loam (5), sandy clay loam (1) in grassland/pasture (2), shrubland (3), open woodland (3).

Food types: No quantitative assessment; DBRU collection records on dung of cattle (7), wildebeest (1).

Temporal activity: Flight activity unknown, but presumably in darkness like other *Pedaria* species; seasonal activity primarily in the summer rainy season (Oct. to May).

Ecoregions Namibia, Botswana: Southern African Bushveld (AT0717), Zambezian Baikiaea Woodlands (AT0726).

Bioregions South Africa: Centred on Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 127 365 km^2 (gross estimate); apparently widespread in various open vegetation types, on various soil soils types and on ruminant herbivore dung, but quantitative support lacking; assessed as Least Concern (LC), but essentially Data Deficient (DD).

Conservation measures: Asessment of conservation status would be improved by quantitative data on ecological associations; protected in uMkhuze, Hluhluwe–iMfolozi and Langjan game reserves (South Africa).

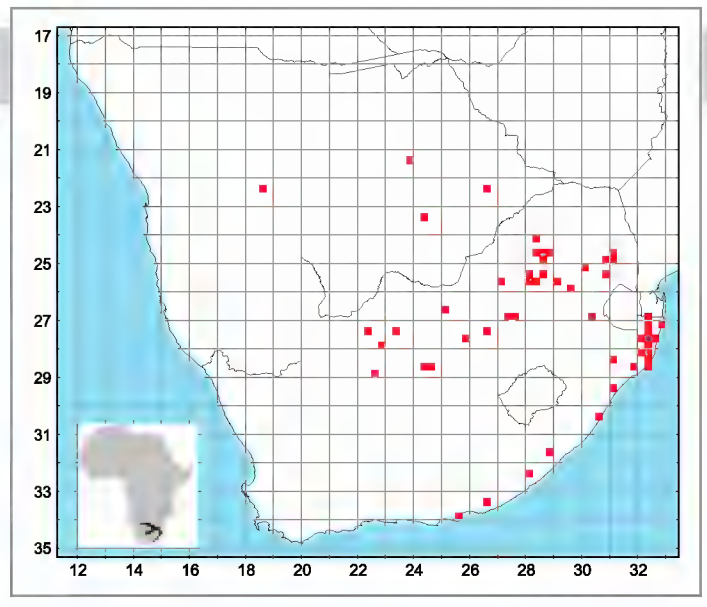
Pedaria picea

Fahraeus, 1857

= *Pedaria cuprascens* Harold, 1859
= *Pedaria sobrina* Péringuey, 1901

Global: LC
Endemic: RSA, Botswana, Namibia

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: *P. picea*: 'prope fluvium Gariep' [near Orange River, South Africa]; *P. cuprasacens*: 'Cap der guten Hoffnung" [Cape of Good Hope, South Africa]; *P. sobrina*: 'Cape Colony (Graham's Town, Port Elizabeth)' [Eastern Cape, South Africa].

Taxonomy: Accepted species.

Distribution: Mostly moist, upland and coastal, southern African sandy savanna: South Africa, Botswana, Namibia; uncommon in central Kalahari, Botswana.

Locality data (mean ± SD, range): Altitude: 860 ± 525, 0–1 759 m; annual rainfall: 664 ± 185, 245–1 003 mm; annual temperature (max. + min. /2): 19.3 ± 2.0, 13.9–22.6°C (N=73).

Habitat: In Gauteng bushveld (as *Pedaria* sp. b): extreme bias to deep sand (753) compared to sandy clay loam (1) with a bias to more open vegetation, grassland (347), open woodland (344), shaded thickets (63); in uMkhuze Game Reserve: extreme bias to deep sand (17.4) compared to duplex soil (sand over clay: 0.4), sandy clay loam (0), clay (0); largely supported by DBRU collection records: sand (6), sandy loam (5), sandy clay loam (3) in grassland/pasture (9), open shrub / woodland (6) and thicket (1).

Food types: In Gauteng bushveld (as *Pedaria* sp.): bias to omnivore dung (pig: 67) compared to herbivore dung (horse: 22, cattle: 44); somewhat similar in Botswana (pig: 17, elephant: 4, cattle: 0); DBRU collection records on dung of cattle (10), human (1).

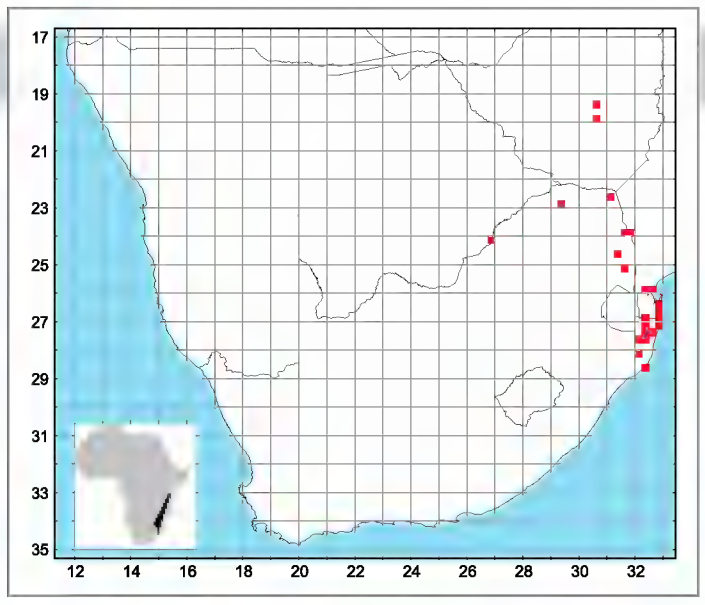
Temporal activity: Flight activity in darkness during the summer rainy season (Oct. to May); on Gauteng bushveld: seasonal activity peak, Oct. to Jan., declining from Feb. to Apr. with mainly evening flight in mid-summer (Nov. and Jan.: 18:00–20:00, fewer 20:00–22:00), but also minor pre-dawn flight activity (04:00–06:00).

Ecoregions Namibia, Botswana: E Kalahari Acacia-Baikiaea Woodlands (AT0709), NE Kalahari Xeric Savanna (AT1309).

Bioregions South Africa: Eastern Kalahari Bushveld (SVk), cooler, moister parts of Central Bushveld (SVcb) and Lowveld (SVl) (Savanna Biome); warmer N or E sandy parts of Dry Highveld Grassland (Gh), Mesic Highveld Grassland (Gm), Sub-Escarpment (Grassland (Gs) (Grassland Biome); Indian Ocean Coastal Belt Biome (CB), Albany Thicket Biome (AT).

Assessment rationale: EOO = 388 675 km^2; AOO would be smaller and restricted according to occurrence of sandy soils within EOO; however, equally abundant in grassland and open woody habitats; conflicting dung association data, but probably comes readily to dung of domestic livestock; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by resolution of conflict in dung associations; protected in uMkhuze Game Reserve, Leeuwfontein and Tswaing nature reserves (South Africa).



Pedaria segregis

Péringuey, 1901

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Mozambique (Rikatla)' [Ricatla, S Mozambique].

Taxonomy: Accepted species with a possibly undescribed close relative centred on Kalahari deep sands and outliers.

Distribution: Sandy soils in moist, lowland, grassy savanna along the E seaboard of Africa: South Africa, Mozambique, Zimbabwe, Kenya; also cited from Tanzania; citation from Angola probably an error.

Locality data (mean ± SD, range): Altitude: 213 ± 363, 0–1 354 m; annual rainfall: 704 ± 112, 482–1 003 mm; annual temperature (max. + min. /2): 22.0 ± 1.2, 18.4–23.4°C (N=33).

Habitat: In uMkhuze Game Reserve: extreme bias to deep sand (23.3) compared to duplex soil (sand over clay: 0.6), sandy clay loam (0.1), clay (0); on sand in Maputo Special Reserve: very strong bias to fossil lagoon grassland (10.7 per sample) compared to sand forest patches (large: 0.1, medium: <0.1, small: 0.4) and coastal dune forest (0); largely supported by DBRU collection records: sand (4), sandy loam (2) in grassland/pasture (2), open shrub / woodland (4) and thicket (1).

Food types: No quantitative assessment; DBRU collection records on dung of cattle (3), wildebeest (1), rhinoceros (1), horse (1).

Temporal activity: Flight activity unknown, but presumably in darkness like other *Pedaria* species; seasonal activity in the summer rainy season (Oct. to Apr.).

Ecoregions Zimbabwe, Mozambique: Sandy soils in Maputaland Coastal Forest Mosaic (AT0119), Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Sandy soils in Central Bushveld (SVcb), Lowveld (SVl), Mopane (SVmp) (Savanna Biome); N Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 730 030 km^2 (gross estimate); AOO would be smaller and restricted according to occurrence of sandy soils and more open vegetation within the EOO; well represented in reserves in coastal regions; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on food associations; protected in uMkhuze Game Reserve (South Africa), Maputo Special Reserve (Mozambique).

Genus *Sarophorus* Erichson, 1847b

Type species and designation: *Pedaria tuberculata* Castelnau, 1840, by monotypy.
Synonyms: None.
Last review: Entire genus reviewed by Frolov and Scholtz (2003a); new species added by Frolov (2004), Roets et al. (2017).

The long-established genus, *Sarophorus* Erichson, 1847b, is usually treated as a full genus although Péringuey (1901) treated it as a subgenus of *Pedaria* Castelnau, 1840, with which it has often been confused. Recent authors have identified characters that may justify the separation of two species into another genus although all are currently treated as belonging to a single genus that is endemic to the S part of the Afrotropical region.

Sarophorus currently comprises 12 valid species divided into two species groups. One (*tuberculatus* group) comprises six species centred to the SW in the winter and bimodal rainfall regions of South Africa and at points along the E escarpment in the summer rainfall region. The other (*costatus* group) also comprises six species that are mostly, though not entirely, centred to the NE with most ranges occurring in moist, summer rainfall savanna. Two of these species show ranges entirely outside of South Africa, Botswana or N Namibia in Zimbabwe, Zambia, SE Democratic Republic of the Congo (DRC) or Tanzania.

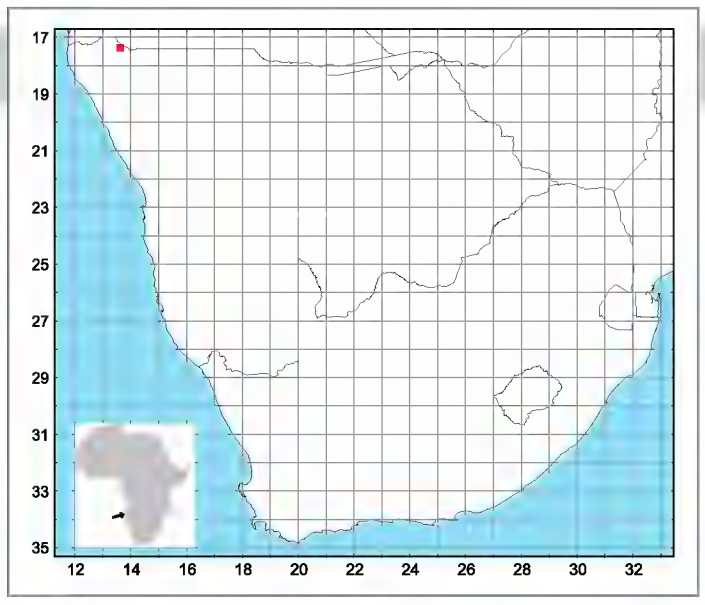
Both species groups overlap either side of the transition between bimodal and summer rainfall areas in the Eastern Cape, South Africa. All species seem to show a bias to denser vegetation providing shade, including forest in the Eastern Cape and KwaZulu-Natal. Such shady or dense vegetation associations suggest clearance of shrubs and trees would be detrimental to population density.

Sarophorus is ecologically poorly known, even though *S. costatus* (Fahraeus, 1857) is frequently attracted to dung-baited pitfalls, particularly to omnivore dung. Of the ten species occurring in southern Africa, eight are restricted to South Africa, one is found in South Africa, Botswana and Zimbabwe with one in N Namibia and Angola.

***tuberculatus* group:** The six group members are centred, respectively, in Renosterveld in Namaqaland (1) or SW Western Cape (1) (may belong to a second genus), shrubland from SW coastal sands of the Western Cape to the Eastern Cape (1), forest patches on the S Cape coast (bimodal rain) (1) or S KwaZulu-Natal (1), or upland woodland in E Mpumalanga (1) (last two both summer rainfall).

***costatus* group:** The four species found in the study region are centred in E savanna (2: but only one widespread), W savanna (1), or on the S coast of the Eastern Cape (summer to bimodal rain) (1).

The four more widely distributed species have been assessed as Least Concern (LC), whereas six known by few records are assessed as Data Deficient (DD) with, in particular, three putative forest or upland woodland species potentially Endangered (EN).



Sarophorus angolensis

Frolov, 2004

No synonyms

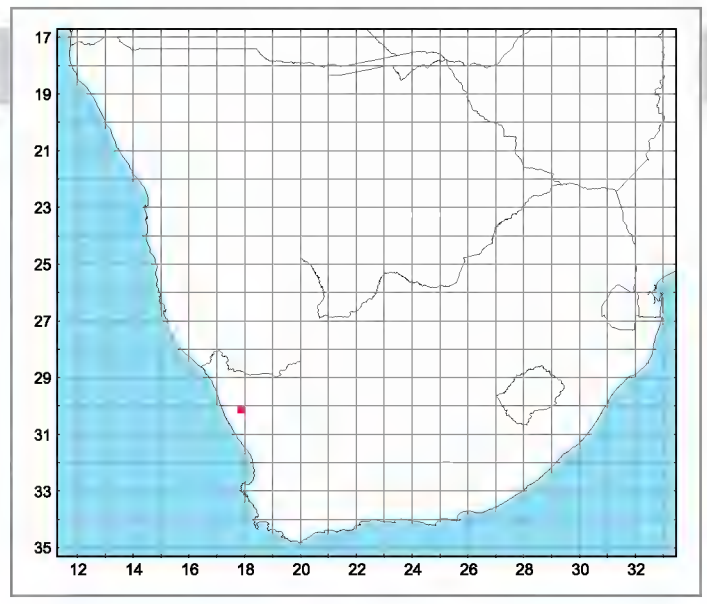
Global: DD

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Tschivinguire Huila' [SW Angola].
Taxonomy: Accepted *costatus* group species; the Namibian material is not yet validated as *S. angolensis* although it is close in appearance.
Distribution: Known from two savanna localities close to the W escarpment: type locality is on the highlands of the Bié Plateau, Huila Province, SW Angola; non-validated locality is at Epembe in the arid Kaokoveld, N Namibia.
Locality data (mean ± SD, range): Altitude: 1 372 ± 581, 961–1 783 m; annual rainfall: 583 ± 289, 379–787 mm; annual temperature (max. + min. /2): 18.2 ± 0.7, 17.7–18.7°C (N=2).
Habitat: No quantitative assessment; Epembe material from white sand near river.
Food types: No quantitative assessment; no data.
Temporal activity: Diel flight periodicity unknown, but probably diurnal; at Epembe, recorded during the late summer rainy season (Feb.); at type locality, recorded in early summer (Nov.).
Ecoregions Namibia: Angolan Mopane Woodlands (AT0702); N Namibian Savanna Woodlands (AT1316).
Assessment rationale: EOO = 3 760 km^2; small range likely a collecting artefact; ecological data virtually absent; alpha taxonomy uncertain as to whether Namibian and Angolan material represents one or two species, currently assessed as Data Deficient (DD).
Conservation measures: A quantitative survey of Kaokoveld and SW Angola is required to determine the EOO, AOO, ecological associations and whether the material comprises one or two species; not currently known from any protected region.

Sarophorus bidentatus

Frolov & Scholtz, 2003a

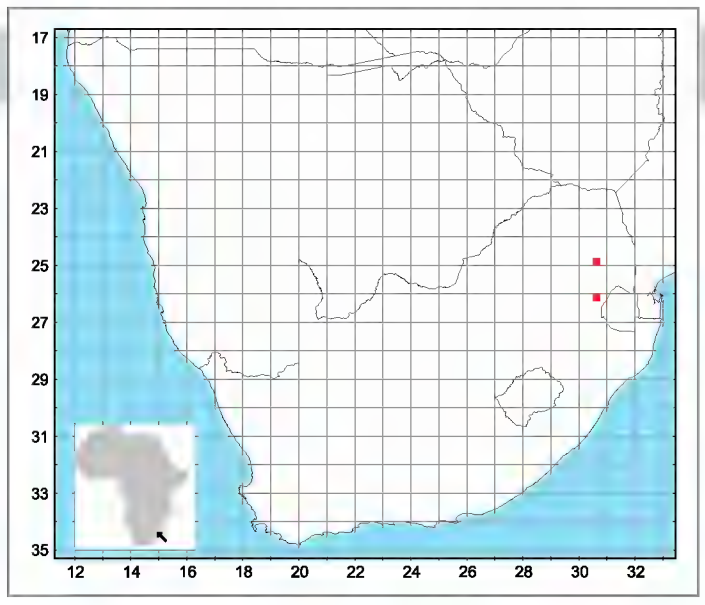


No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Namaqualand, Kamieskroon' [South Africa].
Taxonomy: Accepted *tuberculatus* group species.
Distribution: Currently known from the type locality on the stepped W escarpment of South Africa (holotype) and by a further 14 individuals from 'Cap bon Esp' [Cape of Good Hope] deposited in the Muséum National d'Histoire Naturelle, Paris.
Locality data (average): Altitude: 1 070 m; annual rainfall: 162 mm; annual temperature (max. + min. /2): 15.5°C (N=1).
Habitat: No quantitative assessment; no data available.
Food types: No quantitative assessment; no data available.
Temporal activity: Diel flight periodicity unknown, but probably diurnal in spring (Sept.) during the winter rainy season.
Bioregions South Africa: May be associated with Namaqualand Granite Renosterveld (FRg 1) (Fynbos Biome), which occupies a higher rainfall island within the arid Succulent Karoo Biome; however, survey support required.
Assessment rationale: EOO not known; no ecological data available; single known locality may be inexact; Kamieskroon occurs within the Succulent Karoo at the edge of the upland island of higher rainfall (up to 300–400 mm p/a) within the area of greater aridity; no known records since type specimen was recorded in 1930; close relatives show an association with tall shrubland or shaded thicket and this may be an important consideration for its conservation; currently assessed as Data Deficient (DD) although an IUCN threat category approaching Vulnerable (VU) might be justified on the basis of likely small range and apparent rarity, even though the local Renosterveld is cited as least threatened.
Conservation measures: A survey to determine the full EOO, AOO and ecological associations is required to assess conservation status; not currently known from any reserve.



Sarophorus carinatus

Frolov & Scholtz, 2003a

No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Lydenburg Distr., Ohrigstad' [Mpumalanga, South Africa].
Taxonomy: Accepted *tuberculatus* group species.
Distribution: Known from only two localities along the NE escarpment, South Africa.
Locality data (mean ± SD, range): Altitude: 1 281 ± 142, 1 181–1 382 m; annual rainfall: 875 ± 6, 870–879 mm; annual temperature (max. + min. /2): 16.8 ± 0.9, 16.2–17.4°C (N=2).
Habitat: No quantitative assessment; holotype recorded from humus; another eight individuals retrieved from top soil under leaf litter in a shrub/woodland patch on an upland *koppie* within a grassland matrix.
Food types: No quantitative assessment; food types unknown, but not attracted to pitfalls baited with cattle dung at one locality.
Temporal activity: Diel flight periodicity unknown, but probably diurnal; recorded during the summer rainy season (Nov., Mar.).
Bioregions South Africa: Holotype: Ohrigstad Mountain Bushveld (SVcb 26) (Central Bushveld, Savanna Biome); eight individuals: shrub/woodland patch in KaNgwane Montane Grassland (Gm 16) (Mesic Highveld Grassland, Grassland Biome).
Assessment rationale: EOO = 755 km^2 (presumably underestimated); observations from humus or litter in shrub/woodland suggest the AOO is much more restricted than the EOO, particularly in the Grassland Biome; known from only nine individuals collected in 1962 and 2002 although this may be a collection artefact related to specialised habitat and habits; assessed as Data Deficient (DD), but the small known range at few wooded localities suggests that an IUCN threat category of Endangered (EN) might be justified; however, quantitative data is required in support.
Conservation measures: To assess conservation status, a survey is required to determine the full EOO and AOO, also, to quantify ecological associations; not currently recorded from any protected area.

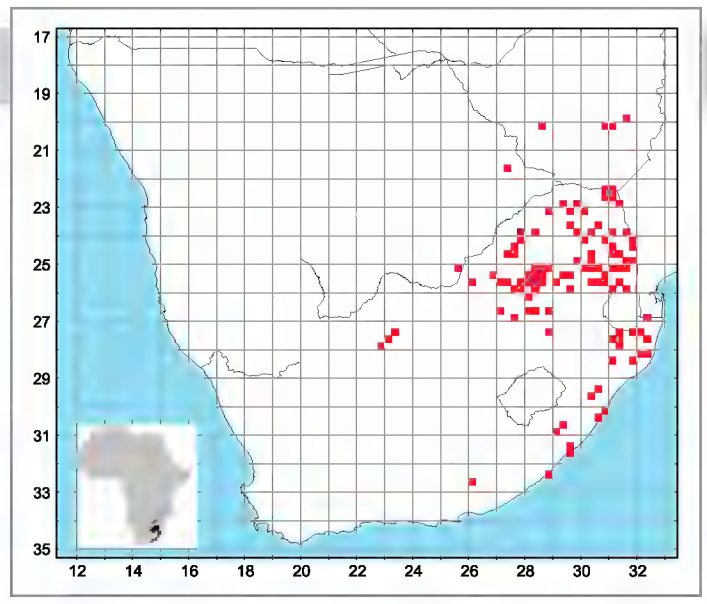
Sarophorus costatus

(Fahraeus, 1857)

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: As *Paedaria costata*: 'in terra Natalensi' [KwaZulu-Natal, South Africa].

Taxonomy: Accepted *costatus* group species.

Distribution: SE African savanna; distribution possibly influenced by woody vegetation cover: South Africa, E Botswana, S Zimbabwe.

Locality data (mean ± SD, range): Altitude: 926 ± 461, 17–1 824 m; annual rainfall: 674 ± 134, 339–1 038 mm; annual temperature (max. + min. /2): 19.3 ± 2.2, 14.5–24.4°C (N=139).

Habitat: In Gauteng bushveld: slight bias to deep sand (251) compared to sandy clay loam (155) and strong bias towards woody vegetation offering at least some shade: grassland (7), open woodland (128), shaded thicket (271); in Suikerbosrand Nature Reserve: recorded only in open woodland (20), not Highveld Grassland (0) or montane grassland (0); on sandy clay loam at Roodeplaat Nature Reserve: bias to open woodland (138), compared to grassland (39) and shaded thicket (18); however, in uMkhuze Game Reserve, extreme bias to finer-grained soils: sand (0.0), sand over clay (1.6), sandy clay loam (46.5), clay (4.7) with a 70% bias to less-shaded vegetation within woodland; DBRU collection records similar: sand (4), sandy loam (15), sandy clay loam (6), clay (1) in grassland / pasture (10), open shrub/woodland (11), shaded woodland/forest (6).

Food types: In Gauteng bushveld: bias to omnivore dung: pig (248), horse (77), cattle (43), carrion (8), rotting grass clippings (8); similar bias at Phalaborwa: pig (62), elephant (11), cattle (16); DBRU collection records reflect commonly sampled dung types: cattle (23), elephant (4), rhinoceros (5), horse (3), human/cattle mix (3).

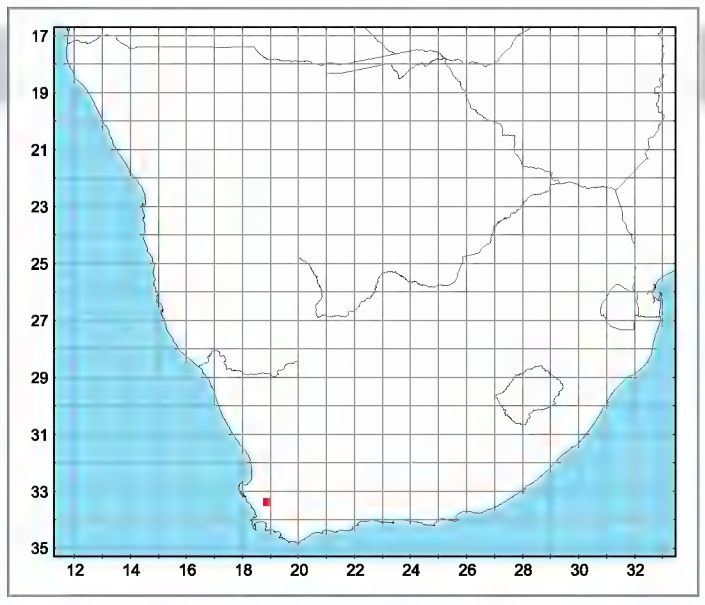
Temporal activity: Diurnal flight activity; sampled in Gauteng bushveld and recorded elsewhere throughout the summer rainy season (Oct. to Apr.); at Phalaborwa: very strong bias to activity in warm weather soon after heavy rainfall (75), little activity in hot, dry weather (12) or warm cloudy weather following light rainfall (2).

Ecoregions Botswana, Zimbabwe: Southern African Bushveld (AT0717), Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl), marginal in Eastern Kalahari Bushveld (SVk) (Savanna Biome); Indian Ocean Coastal Belt Biome (CB); N margins Mesic Highveld Grassland (Grassland Biome); also margins of Sub-Escarpment Savanna (SVs) and Sub-Escarpment grassland (Gs).

Assessment rationale: EOO = 283 960 km^2; evidence for soil and vegetation associations shows some conflict, particularly soil associations; however, it is probable that there is a bias to shade or partial shade; if so, the AOO would be influenced by woody vegetation cover and impacted upon by its clearance, which is extensive in some parts of its range; however, *S. costatus* is widespread and attracted to the dung of farm livestock despite a bias to omnivore dung; therefore, currently assessed as Least Concern (LC).

Conservation measures: To improve the assessment of conservation status, there is a need for further quantitative data on soil and vegetation associations, particularly the relative importance of shade offered by woody vegetation as this could seriously influence AOO; protected in Kruger National Park, uMkhuze and Hluhluwe–iMfolozi game reserves (South Africa).



Sarophorus diabolus

Roets, 2017

No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'SOUTH AFRICA, Western Cape Province, Riebeeck-Kasteel, Porseleinberg, –33.45995 18.88627'.
Taxonomy: Accepted *tuberculatus* group species.
Distribution: Known only from two adjoining Renosterveld localities in the winter rainfall region: SW Western Cape in South Africa.
Locality data (mean ± SD, range): Altitude: 334 ± 112, 255–413 m; annual rainfall: 350 ± 1, 349–351 mm; annual temperature (max. + min. /2): 16.9 ± 0.5, 16.6–17.3°C (N=2).
Habitat: No published quantitative assessment; type series recorded in dense, 2–3 m tall, Renosterveld.
Food types: No quantitative assessment; type series sampled to a combined bait of pig dung and chicken liver.
Temporal activity: Diel flight periodicity unknown, but probably diurnal; type series recorded mainly during the winter rainy season in late winter (July); two individuals also recorded in late summer (March).
Bioregions South Africa: Vegetation unit: Swartland Shale Renosterveld (FRs 9) (West Coast Renosterveld (FO 7), Fynbos Biome).
Assessment rationale: EOO not known; current AOO may be dependent on persistence of dense, tall, Renosterveld shrubland in a widespread vegetation unit that is now 90% totally transformed, primarily as arable farmland; *S. diabolus* would currently qualify for an IUCN threat category approaching Critically Endangered (CR), although it is assessed as Data Deficient (DD) in the absence of a survey to discover other localities.
Conservation measures: A quantitative survey of surviving Renosterveld patches in (FRs 9) and similar vegetation on finer-grained soils in adjoining areas of the Western Cape is essential to determine the full EOO; assessment of conservation status also requires quantitative data on ecological associations, particularly the effects of removal of dense shrubland on the AOO; protected in Kasteelberg Nature Reserve, Western Cape.

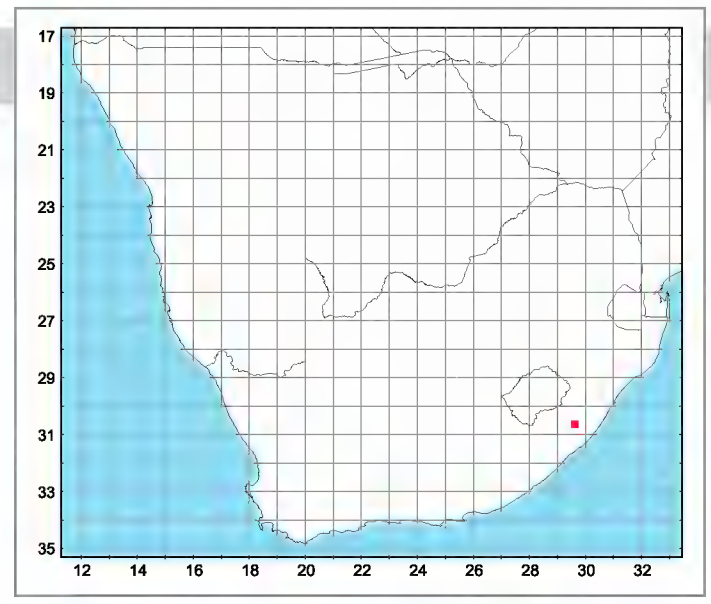
Sarophorus frolovi

Roets, 2017

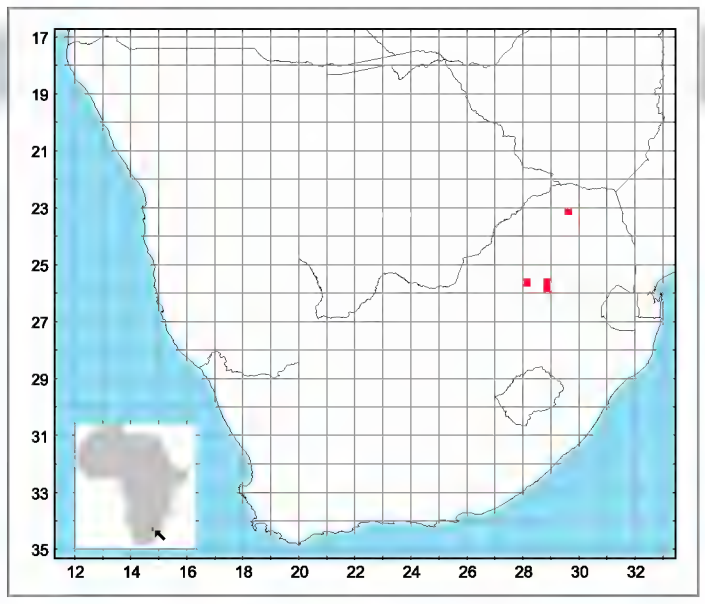
No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: 'SOUTH AFRICA, KwaZulu-Natal Province, Midlands, Weza forestry plantations, –30.61680 29.683626'.
Taxonomy: Accepted *tuberculatus* group species.
Distribution: Known from a single forest locality in the summer rainfall region: S KwaZulu-Natal in South Africa.
Locality data (average): Altitude: 1 187 m; annual rainfall: 815 mm; annual temperature (max. + min. /2): 15.3°C (N=1).
Habitat: No quantitative assessment; type series recorded at edges between Southern Mistbelt Forest and grassland.
Food types: No quantitative assessment; type series sampled to a combined bait of pig dung and chicken liver.
Temporal activity: Diel flight periodicity unknown, but probably diurnal; recorded during the summer rainy season (Feb.).
Bioregions South Africa: Grid reference for type locality coincides with the Midlands Mistbelt Grassland vegetation unit (Gs 9) (Sub-Escarpment Grassland, Grassland Biome) near a patch of Southern Mistbelt Forest (FOz 3) (Forest Biome).
Assessment rationale: EOO and AOO not known; ecologically extremely poorly known; would currently qualify for an IUCN threat category of at least Vulnerable (VU), but in the absence of surveys around other FOz 3 forest patches, currently assessed as Data Deficient (DD).
Conservation measures: A survey in Sub-Escarpment Grassland around other patches of FOz 3 is required to determine the full EOO of *S. frolovi*; assessment of conservation status also requires quantitative data on ecological associations, particularly relative abundance in forest patches versus that in grassland; unclear if *S. frolovi* is protected under Weza Plantation management.



Sarophorus latus

Frolov & Scholtz, 2003a

No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Farm Rhenosterpoort' [Gauteng, South Africa].
Taxonomy: Accepted *costatus* group species; although close in appearance to *Sarophorus costatus* (Fahraeus, 1857), the aedeagus is quite different.
Distribution: Bushveld savanna in the vicinity of E–W trending mountain ranges (Magaliesberg; Soutpansberg), South Africa.
Locality data (mean ± SD, range): Altitude: 1 091 ± 165, 956–1 331 m; annual rainfall: 633 ± 40, 594–689 mm; annual temperature (max. + min. /2): 19.0 ± 0.9, 17.8–19.5°C (N=4).
Habitat: No quantitative assessment; no data available.
Food types: No quantitative assessment; recorded on carrion (dead bird) plus dung of baboon and horse.
Temporal activity: Diel flight periodicity unknown, but probably diurnal; recorded during the summer rainy season (Dec. to Apr.).
Bioregions South Africa: Vegetation units: Moot Plains Bushveld (SVcb 8), Loskop Mountain Bushveld (SVcb 13), Soutpansberg Mountain Bushveld (SVcb 21) (Central Bushveld Bioregion, Savanna Biome).
Assessment rationale: EOO = 12 270 km^2 (includes areas between mountain ranges); AOO may be restricted to mountain bushveld, but quantitative support required; could be susceptible to habitat transformation (28%, SVcb 8; 3%, SVcb 13; 21%, SVcb 21), but no accurate data on vegetation associations; assessed as Data Deficient (DD) although it may currently warrant an IUCN threat category of Vulnerable (VU) on the basis of restricted range at few known locations.
Conservation measures: To assess conservation status, a quantitative survey of mountain bushveld and adjoining vegetation units is required to determine the EOO, AOO and ecological associations; protected in Happy Rest and Rhenosterpoort nature reserves.

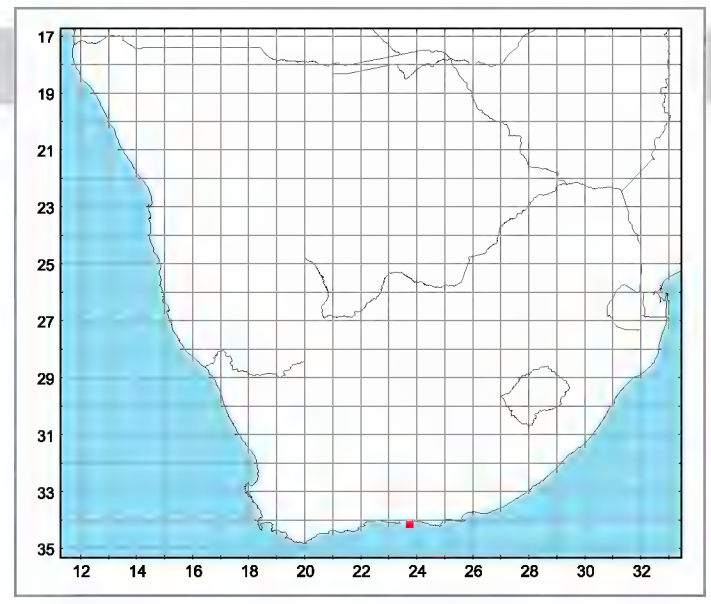
Sarophorus punctatus

Frolov & Scholtz, 2003a

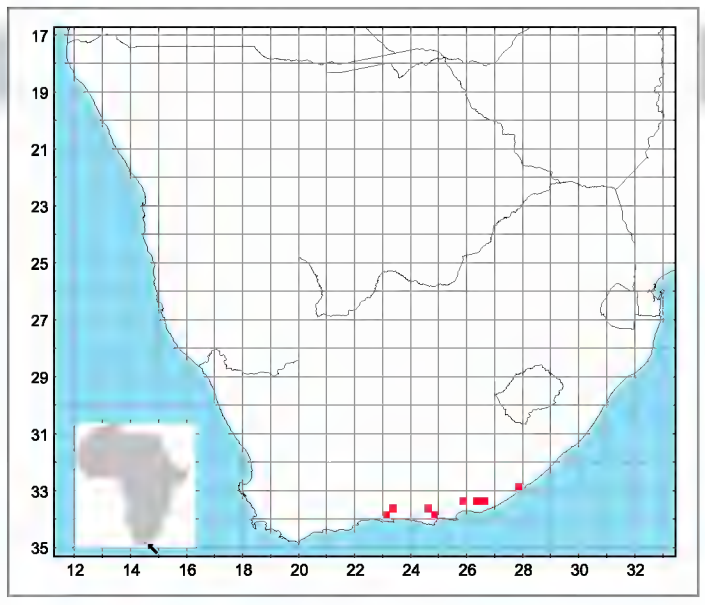
No synonyms

Global: EN (see IUCN Red List – EN)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: 'Keurboomstrand' [Eastern Cape, South Africa].
Taxonomy: Accepted *tuberculatus* group species.
Distribution: Known only from the type locality on the coastline of the Eastern Cape, South Africa.
Locality data (average): Altitude: 0 m; annual rainfall: 458 mm; annual temperature (max. + min. /2): 18.0°C (N=1).
Habitat: No adequate quantitative assessment; sampled using ground traps set from the edge into disturbed podocarp forest.
Food types: No quantitative assessment; unknown.
Temporal activity: Diel flight periodicity unknown, but probably diurnal; recorded during mid-summer (Dec.) in the bimodal rainfall region.
Bioregions South Africa: Sampled from Southern Afrotemperate Forest (FOz 1) (Forest Biome) although grid reference coincides with adjoining South Outeniqua Sandstone Fynbos (FFs 19) (Fynbos Biome).
Assessment rationale: EOO and AOO not known, but AOO possibly dependent on patches of forest along the Eastern Cape coastline, established on sandstone and granite-derived soils; essentially Data Deficient (DD) although tentatively assessed as Endangered (EN) in line with current IUCN Red List, which focuses on the low number of known individuals from a single locality recorded ~40 years ago (1976); further data are required for a more accurate assessment.
Conservation measures: Assessment of conservation status as EN needs to be supported by a survey of habitats at the type locality and of similar habitats at distance from Keurboomstrand; this study should determine the EOO, AOO, ecological associations and current levels of threat; elements of FOz 1 are now protected in Garden Route National Park close to the type locality.



Sarophorus striatus

Frolov & Scholtz, 2003a

No synonyms

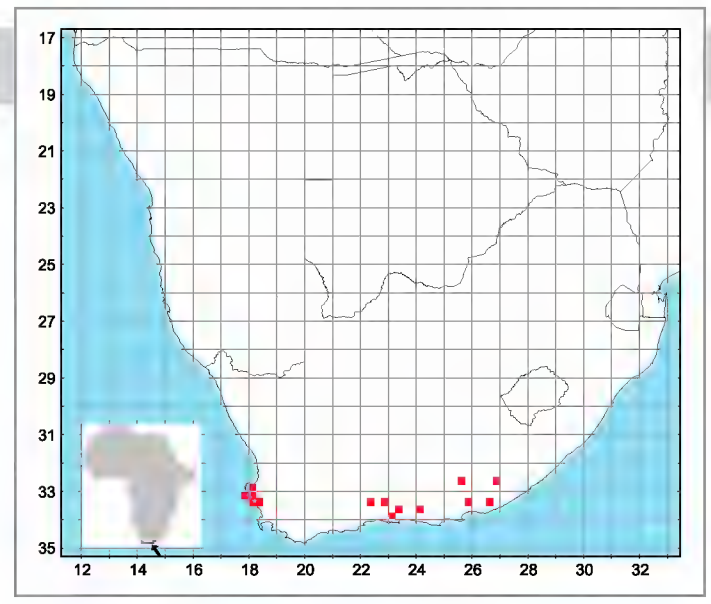
Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: '23 km S of Avontuur' [Eastern Cape, South Africa].
Taxonomy: Accepted *costatus* group species.
Distribution: Centred on Albany Thicket along the S coastal region of the Eastern Cape, South Africa.
Locality data (mean ± SD, range): Altitude: 371 ± 248, 27–871 m; annual rainfall: 501 ± 100, 390–741 mm; annual temperature (max. + min. /2): 17.2 ± 1.1, 15.0–19.2°C (N=13).
Habitat: No quantitative assessment; limited DBRU collection records inconclusive: sandy loam (2), sandy clay loam (1) in grassland/pasture (2), open woodland (1).
Food types: No quantitative assessment; DBRU collection records all from cattle dung (6).
Temporal activity: Diel flight periodicity unknown, but probably diurnal; recorded in late summer and during the autumn peak (Jan. to May) of the bimodal rainy season.
Bioregions South Africa: Vegetation units: Gamtoos Thicket (AT 4), Sundays Thicket (AT 6), Kowie Thicket (AT 8), Albany Coastal Belt (AT 9) (Albany Thicket Biome); also Bhisho Thornveld (SVs 7) (Sub-Escarpment Savanna); Kouga Sandstone Fynbos (FFs 27), Langkloof Shale Renosterveld (FRs 17) (Fynbos Biome).
Assessment rationale: EOO = 6 740 km^2; relatively limited known range; vegetation associations unclear, but some relatives are shade specialists; therefore, as this species is centred on a thicket biome, clearance of thicket may be detrimental to population density and/or lead to reduced AOO; however, quantitative support required; current transformation in thicket stands at 6–17% (AT 4, AT 6, AT 8, AT 9), mainly due to cultivation and urbanisation; currently assessed as Least Concern (LC) although a quantitative assessment is recommended.
Conservation measures: Assessment of conservation status would be much improved by quantitative data on ecological associations, particularly if there is a bias to shade and a threat due to clearance of woody vegetation; not currently known from any protected area.

Sarophorus tuberculatus

(Castelnau, 1840)



No synonyms

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Pedaria tuberculata*: 'Afrique' [Africa].
Taxonomy: Accepted *tuberculatus* group species.
Distribution: SW Western Cape and Eastern Cape in the winter and bimodal (spring/autumn) rainfall regions, South Africa; disjunction between W/E localities possibly a collection artefact.
Locality data (mean ± SD, range): Altitude: 445 ± 464, 0–1 383 m; annual rainfall: 386 ± 119, 242–667 mm; annual temperature (max. + min. /2): 15.9 ± 1.2, 13.2–18.0°C (N=17).
Habitat: No adequate quantitative assessment; in Western Cape: sampled on both sand (45) and sandy loam (73) in tall shrubland at Farm Pampoenvlei, but absent from low profile scrub on deep sands of nearby coastal plain (Farm Modderrivier); also sampled on deep sand in tall shrubland (69) at Farm Geelbek, but rare in adjoining sparse pasture cleared of shrubs (2); supported by limited DBRU collection records from sand (3), sandy loam (1), sandy clay loam (1) in grassland (1) and shrubland (5).
Food types: No quantitative assessment, but sampled to cattle dung in Western Cape; DBRU collection records entirely from dung of cattle (8), but quantitative assessment required.
Temporal activity: Diel flight periodicity unknown, but probably diurnal and primarily in spring (July to Oct.) and autumn (Mar. to May) in the winter and bimodal rainy seasons; at farms Geelbek and Pampoenvlei in Western Cape: limited late July activity, but primarily active in Aug., declining in Sept. and rare in Oct., also rare autumn activity in May.
Bioregions South Africa: In the W: Strandveld (FS 3, FS 5), Granite Renosterveld (FRg 2); in the E: Sand Fynbos (FFs 19, FFs 23, FFs 27) (all Fynbos Biome); also Albany Thicket Biome (AT).
Assessment rationale: EOO = 46 695 km²; available ecological data suggest the AOO would be much smaller according to occurrence of tall shrubland, which is under particular threat in the W (transformation in the E: 2–28% in FFs 19, FFs 23, FFs 27; W: 35-80% in FS 3, FS 5, FRg 2); food associations not tested, but clearly attracted to dung of farm livestock; currently assessed as Least Concern (LC) on basis of large EOO and protection in at least one reserve in the W.
Conservation measures: Assessment of conservation status would be improved by further quantitative ecological data, particularly the effects of shrubland clearance; protected on Farm Geelbek, which is now part of West Coast National Park where the sparse grassland pasture has been permitted to regenerate as shrubland.

TRIBE CANTHONINI

van Lansberge, 1874a

[TRIBE DELTOCHILINI Lacordaire, 1856]

As Deltochilides; Type genus: *Deltochilum* Eschscholtz, 1822.

As Canthonides; Type genus: *Canthon* Hoffmansegg, 1817.

Synonyms:

= Minthophilides Lacordaire, 1856; Type genus: *Mentophilus* Castelnau, 1840.
= Scatonomides Lacordaire, 1856; Type genus: *Scatonomus* Erichson, 1835.
= Epilissinides van Lansberge, 1874; Type genus: *Epilissus* Dejean, 1836.
= Coprobiadae Burmeister, 1873; Type genus: *Coprobius* Latreille, 1829 [= syn. of *Canthon* Hoffmansegg, 1817].
= Epirinides van Lansberge, 1874a; Type genus: *Epirinus* Dejean, 1833 (revalidated as tribe Epirinini van Lansberge, 1874a (Daniel et al. 2020)).
= Panelini Arrow, 1931; Type genus: *Panelus* Lewis, 1895.

Although the tribal name, Deltochilini, takes precedence (Bouchard et al. 2011), according to Smith (2006), Canthonini should be maintained as the tribal name through long-term common usage. As a result, either Deltochilini, Canthonini or both have been cited as the tribal name in recent publications. Even the recent partial tribal revision of Tarasov and Dimitrov (2016) will not easily resolve this controversy as the closely related type genera, *Deltochilum* and *Canthon* (Monaghan et al. 2007), occur in the same Neotropical and Nearctic clade now designated as the tribe, Deltochilini (Canthonini) *sensu novo*.

In the old sense, Canthonini are globally represented within areas of tropical, warm temperate and winter rainfall climate. However, global molecular phylogeny clearly shows that the current tribal membership is polyphyletic at generic level with seven distantly related, major lineages for just 36% of the tribal generic-level membership (Monaghan et al. 2007) and at least 14 lineages in the recent partial tribal revision of Tarasov and Dimitrov (2016). As a result, their redefinition of the tribe as Deltochilini (Canthonini) *sensu novo* comprises much reduced membership restricted to the Americas. Some American and all non-American genera (Africa, Madagascar, Oriental, Australasia) are given the status of *incertae sedis*. Under these circumstances, we retain the old classfication system for arranging the genera in this book, pending a full tribal revision.

At the present time, 101 genera are assigned to the old tribe on morphological criteria. These primarily occur in four continental biogeographical centres (Africa: 27; Oriental: 4; Americas/Caribbean: 31; Australia/New Guinea: 19) with limited sharing: Africa/Oriental (1), Afro-Eurasia (1). A number of genera are endemic to islands: Madagascar (7), Mauritius (1), New Caledonia (8), New Zealand (2).

Of the 27 genera and 90 species recorded for the Canthonini (old sense) in the Afrotropical region, most are restricted to arid and winter rainfall regions of the SW or in forests and upland grasslands along the S and E seaboards as far as SE Kenya. Essentially, only one canthonine genus is widely represented in the African tropics (*Chalconotus* Dejean, 1833: 9 spp.) although two others have limited spot representation in W Africa and/or NE Africa (*Odontoloma* Boheman, 1857: 20 spp.; *Pycnopanelus* Arrow, 1931: 2+1 Oriental spp.). Past doubts have been expressed concerning the inclusion of some of these genera in the Canthonini (Scholtz & Howden, 1987: *Pycnopanelus*; Howden & Scholtz, 1987: *Odontoloma*).

A total of 23 canthonine genera and 76 species are represented in South Africa, Botswana and Namibia, although none of these belong to the tribe in the new sense. *Chalconotus* and *Pycnopanelus* are represented in all three countries, *Dicranocara* Frolov & Scholtz, 2003b, and *Odontoloma* are shared between Namibia and South Africa, *Gyronotus* van Lansberge, 1874a (8 spp.) occurs along the E seaboard from South Africa to Tanzania. The remaining genera are found only in Namibia (5) or South Africa (13).

Molecular phylogeny suggests that 18 of these 23 genera represent seven distinct lineages (Mlambo et al. 2015, Tarasov & Dimitrov 2016). In rank order from most basally to most terminally derived, the generic lineages are typified by (numbers of southern African species in brackets):

(1) A branched clade, now comprising three new tribes (Davis et al. 2019):

- **(A)** Extremely small-bodied *Odontoloma* (15) mostly centred in southern Africa (now in the new tribe Odontolomini Davis, Deschodt & Scholtz, 2019).
- **(B)** Arid SW seaboard genera: *Byrrhidium* Harold, 1869a (2); *Dicranocara* Frolov & Scholtz, 2003 (4); *Namakwanus* Scholtz & Howden, 1987 (2); that may be associated with rock hyrax middens or concentrations of dung (now in the new tribe Byrrhidiini Davis, Deschodt & Scholtz, 2019).
- **(C)** SE seaboard forest litter genera: *Outenikwanus* Scholtz & Howden, 1987 (1); *Silvaphilus* Roets & Oberlander, 2010 (1); *Endroedyolus* Scholtz & Howden, 1987 (1); *Aliuscanthoniola* Deschodt & Scholtz, 2008 (1); *Peckolus* Scholtz & Howden, 1987 (3) (now in the new tribe Endroedyolini Davis, Deschodt & Scholtz, 2019).

(2) *Circellium* Latreille, 1829 (1) in sandy winter and bimodal rainfall shrubland, S coast, South Africa with close relationships to Scarabaeini.

(3) E seaboard genus (South Africa to SE Kenya), *Gyronotus* van Langsberge, 1874 in South African and Eswatini forest patches or moist, cool grasslands (5).

(4) *Bohepilissus* Paulian, 1975, in S coast forest litter, South Africa (2) with close relationships to some Madagascar, Neotropical and Australian genera.

(5) *Chalconotus* Dejean, 1833 (cited as *Anachalcos* Hope, 1837) (1); single savanna species distributed from S to E to W Africa.

(6) *Epirinus* Dejean, 1833 (29) in cooler South African climates: upland NE grassland and SW shrubland, SE forests, SW winter and bimodal rainfall shrubland; transferred to the tribe Sisyphini *sensu novo* by Tarasov and Dimitrov (2016) but removed to the revalidated tribe, Epirinini van Lansberge, 1874a, by Daniel et al. (2020).

(7) Less typical canthonines in the arid SW: *Pycnopanelus* Arrow, 1931 (1); desert sands on the SW seaboard: *Hammondantus* Cambefort, 1978 (1); or shrublands of the SW winter rainfall region: *Aphengoecus* Péringuey, 1901 (2); plus, surprisingly, one SE forest litter genus: *Dwesasilvasedis* Deschodt & Scholtz, 2008 (1) grouped together with Lineage 4 Coprini genera, *Macroderes* Westwood, 1842 (SW Cape), *Xinidium* Harold, 1869a (SE highlands).

Several genera are missed from these phylogenies; two SE forest litter genera: *Nebulasilvius* Deschodt & Scholtz, 2008 (2), *Parvuhowdenius* Deschodt & Scholtz, 2008 (1) (= new tribe: Endroedyolini); three arid SW seaboard genera: *Versicorpus* Deschodt, Davis & Scholtz, 2011 (2), *Drogo* Deschodt, Davis & Scholtz, 2016 (1), *Namaphilus* Deschodt & Davis, 2017 (3) (= new tribe: Byrrhidiini).

The recent global phylogeny and partial tribal revision of Tarasov and Dimitrov (2016) largely supports the divisions of Mlambo et al. (2015), but the lineages are more widely separated in the global analysis by taxa from other biogeographical regions. Tarasov and Dimitrov (2016) classify Lineage 1 (above) as 'Basal Scarabaeinae' along with most African genera of the Ateuchini (old sense), except *Pedaria*. Lineages 2 to 6 are also in separarate lineages with *Epirinus* removed to the tribe Sisyphini (but see notes under (6) above). The genera of Lineage 7 are separated into four neighbouring lineages along with *Macroderes* and *Xinidium*, here included in the Coprini (old sense).

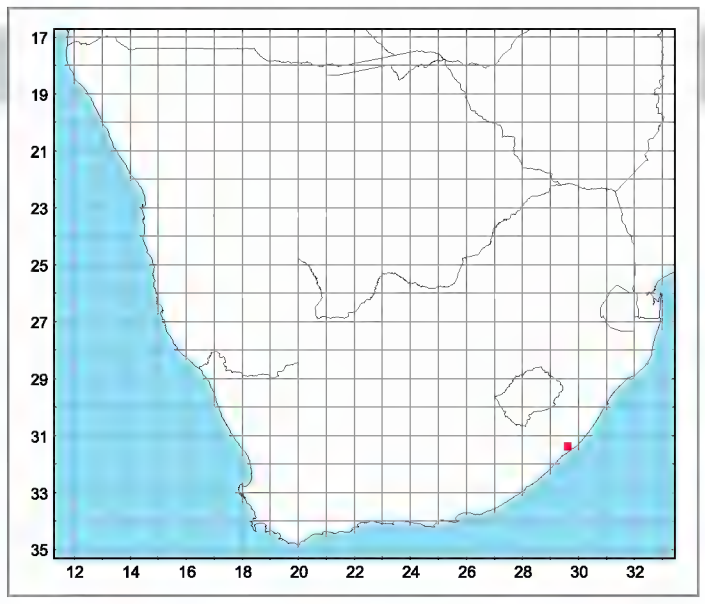
Membership of this polyphyletic tribe (old sense) is frequently characterised by ball-rolling behaviour, although in southern Africa this has been observed only in larger-bodied genera such as *Circellium* and *Chalconotus* or in genera of smaller body size such as *Epirinus*. Different habits are probably shown by most genera (see *Dicranocara*; also tunnelling observed in *Aphengoecus*). Habits of those genera showing smallest body size are unknown, including *Odontoloma* and those many genera found in forest litter along the S and SE seaboard.

Most flightless species with small ranges in South African fynbos and forest are assessed as facing threats (Critically Endangered (CR): 1; Endangered (EN): 6; Vulnerable (VU): 17) including a few flying species (VU: 4).

Genus *Aliuscanthoniola* Deschodt & Scholtz, 2008

Type species and designation: *Aliuscanthoniola similaris* Deschodt & Scholtz, 2008, by original designation.
Synonyms: None.
Last review: Genus created by Deschodt and Scholtz (2008).

Aliuscanthoniola Deschodt & Scholtz, 2008 is monotypic and is currently known from only a single small patch of forest on the SE coast of South Africa. In view of the very small range at a single known threatened locality, it is currently assessed as Endangered (EN).



Aliuscanthoniola similaris

Deschodt & Scholtz, 2008

No synonyms

Global: EN
Endemic: RSA

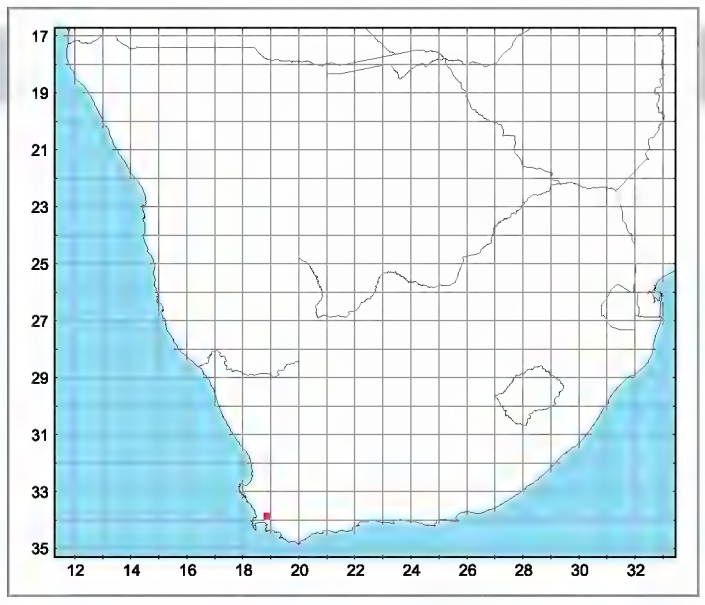
J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'S. Afr.; Transkei, Ntsubane For. St.' [Ntsubane Forest Station, Eastern Cape, South Africa].
Taxonomy: Accepted species.
Distribution: Known only from Ntsubane Forest, an element of the Critically Endangered Scarp Forest on the Pondoland coast.
Locality data (average): Altitude: 55 m; annual rainfall: 961 mm; annual temperature (max. + min. /2): 19.7°C (N=1).
Habitat: No quantitative assessment; recorded on finer-grained soils in forest leaf litter.
Food types: Not known.
Temporal activity: Flightless; diel periodicity unknown; recorded during the summer rainy season (Nov., Dec.)
Bioregions South Africa: A single patch of the Scarp Forest vegetation unit (FOz 5) (Forest Biome).
Assessment rationale: EOO not known but type was recorded from an irregular forest patch comprising only 61.1 km^2; Ntsubane is significantly threatened by utilisation of resources and peripheral fires; in view of the small known range at a single threatened location, assessed as Endangered (EN).
Conservation measures: Continuing preservation of Ntsubane State Forest (94.46 km^2) is essential for the protection of the monotypic genus, *Aliuscanthoniola*; as the EOO and AOO might extend southwestwards to other nearby forest patches around Port St Johns, investigation of these forests would be advantageous, particularly as all are similarly threatened.

Genus *Aphengoecus* Péringuey, 1901

Type species and designation: *Aphengoecus clypeatus* Péringuey, 1901, by monotypy.
Synonyms: None.
Last review: Entire genus reviewed by Scholtz and Howden (1987).

Aphengoecus Péringuey, 1901, comprises two flightless species of uncertain habits that are restricted to the SW of the Western Cape. The possibility of association with termite nests needs to be investigated. In view of their small ranges and/or low frequency of records in an area of high habitat modification, they presumably face threats. Available data result in assessments of either Vulnerable (VU) or Data Deficient (DD).



Aphengoecus clypeatus

Péringuey, 1901

No synonyms

Global: DD
Endemic: RSA

| J | A | S | O | N | D | J | F | M | A | M | J |

Type locality: 'Cape Colony (Stellenbosch)' [Western Cape, South Africa].
Taxonomy: Accepted species.
Distribution: Known only from the type locality of Stellenbosch and inexact localities cited from the Cape and southern Africa.
Locality data (average): Altitude: 228 m; annual rainfall: 435 mm; annual temperature (max. + min. /2): 16.9°C (N=1).
Habitat: Not known, but dominant natural habitat in two vegetation units around Stellenbosch is shrubland on sandy loam.
Food types: Possibly associated with the refuse heaps of termites whose nests were close to the traps that captured the type series of 27 individuals; not recorded elsewhere in the study area.
Temporal activity: Flightless, nocturnal activity; seasonal activity unknown.
Bioregions South Africa: Stellenbosch lies in the West Renosterveld Bioregion (FO 7) (Fynbos Biome) at the edge of two vegetation units, Swartland Granite Renosterveld (FRg2) and Swartland Shale Renosterveld (FRs 9).
Assessment rationale: EOO unknown; only known by the type series, collected in 1892, and nine other individuals; unclear if subsequent absence of collection is due to specialised habits or radical habitat transformation in the Stellenbosch area (FRg 2: 80%; FRs 9: 90%); assessed as Data Deficient (DD), but these circumstances probably warrant at least an Endangered (EN) threat category, probably Critically Endangered (CR).
Conservation measures: A survey needs to be mounted in the Stellenbosch region to determine if this species is still extant; if rediscovered, its EOO, AOO and ecological associations need to be determined to assess conservation status; sampling in the vicinity of termite mounds would be recommended; not known from any protected area.

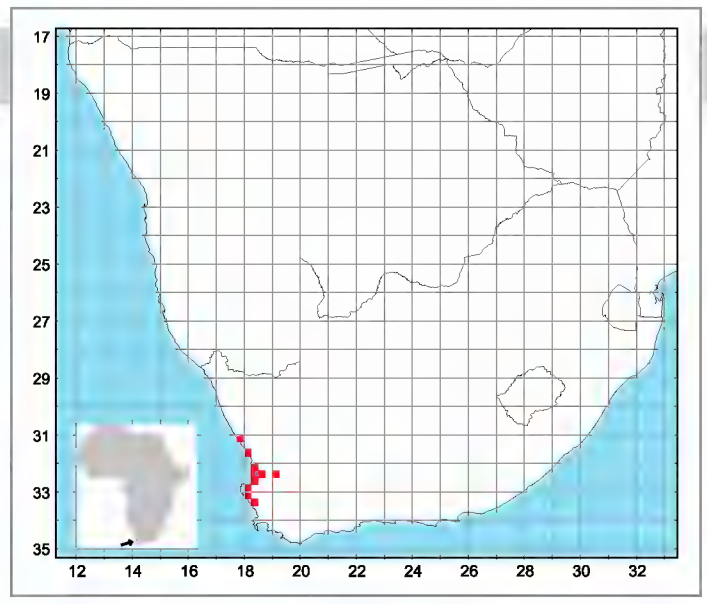
Aphengoecus multiserratus

Scholtz & Howden, 1987

No synonyms

Global: VU
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: 'Cape, Cederberg, Jeep track, 1 280 m' [Western Cape, South Africa].
Taxonomy: Accepted species.
Distribution: Restricted to a small area along the dry SW coastline of the Western Cape, South Africa and adjoining dry mountains (Cederberg).
Locality data (mean ± SD, range): Altitude: 194 ± 298, 3–1 280 m; annual rainfall: 245 ± 64, 146–350 mm; annual temperature (max. + min. /2): 17.1 ± 0.9, 15.2–18.5°C (N=16).
Habitat: Sampled only on deep sand in natural shrubland: on dunes at Farm Pampoenvlei (31), in strandveld at Farm Modderrivier (9).
Food types: Attracted in small numbers to faeces, cattle dung, meat and banana bait.
Temporal activity: Flightless, diel periodicity unknown; at S edge of range: quantitative data for seasonal activity strongly biased to autumn tailing off into winter (Apr. to July); strong bias to spring (Aug., Sept.) in reference material, but from traps left 59–63 days.
Bioregions South Africa: Centred on Western Strandveld (FS) and Sand Fynbos (FFd) vegetation units along the coast and in Sandstone Fynbos (FFs) on the Cederberg (Fynbos Biome); also in Namaqualand Strandveld (SKs 7) at the S end of the Succulent Karoo Biome.
Assessment rationale: EOO = 3 700 km^2; occurs on the coastal strip of the farm, Modderrivier, run as the private Grotto Bay Nature Reserve, but little of the known range coincides with officially protected areas; furthermore, there is high habitat transformation across its small range (FS, FFd: 25–55%; FFs: 15%); an EOO < 20 000 km^2 and AOO probably < 2 000 km^2 at a limited number of locations in an area subject to extensive transformation would qualify this species for Vulnerable (VU) status.
Conservation measures: In view of possible ecological specialisation, probable low vagility due to flightless habits, and limited protection in reserves, a study of its AOO and ecological associations is required to better assess conservation status; owing to observations made on the habits of its congener, *A. clypeatus* Péringuey, 1901, possible association with the refuse heaps of termites or ants should be investigated; not recorded in West Coast National Park, but protected in the Cederberg Wilderness Area.

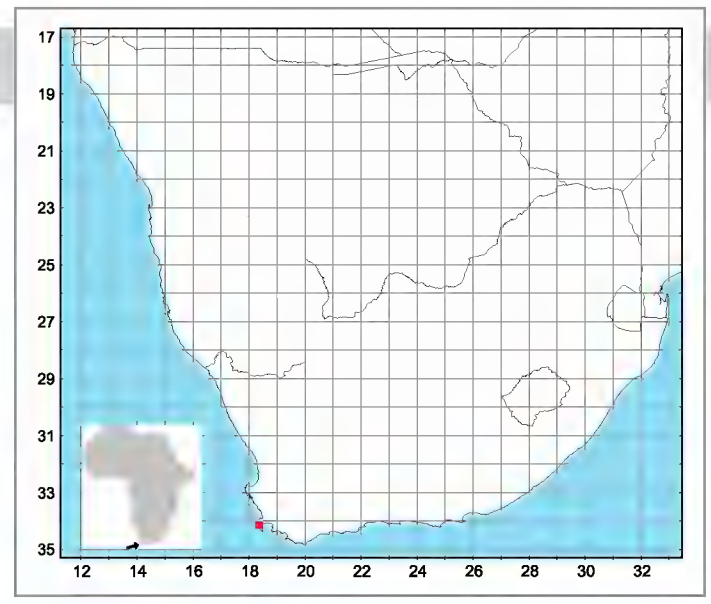
Genus *Bohepilissus* Paulian, 1975

Type species and designation: *Epilissus subtilis* Boheman, 1857, by original designation.
Synonyms: None.
Last review: Entire genus reviewed by Scholtz and Howden (1987).

Bohepilissus Paulian, 1975, currently comprises two very small-bodied, flightless, forest endemic species. One shows a restricted range in the highly modified SW Cape and is assessed as Vulnerable (VU). The other is widespread in forest patches along the S and SE coasts, but may represent a species complex. Both have been recorded in forest litter.

Bohepilissus nitidus

(Balthasar, 1965a)

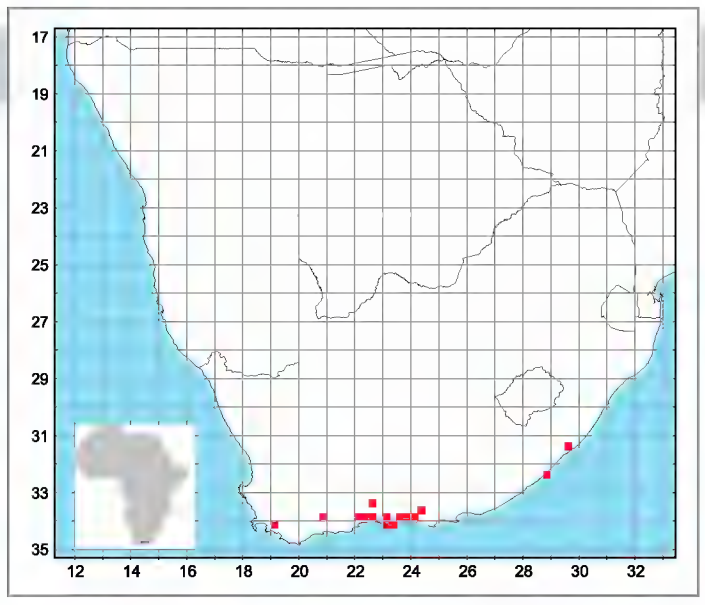


No synonyms

Global: VU
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Panelus nitidus* 'Süd-Afrika aus der Umgebung von Kapstadt' [environs of Cape Town, Western Cape, South Africa].
Taxonomy: Accepted species.
Distribution: South Africa, Western Cape, Cape Town: primarily E slopes of Table Mountain with one record from a mountainside at Muizenberg.
Locality data (mean ± SD, range): Altitude: 485 ± 376, 93–994 m; annual rainfall: 487 ± 63, 415–555 mm; annual temperature (max. + min. /2): 14.1 ± 1.8, 11.7–16.1°C (N=6).
Habitat: Probably primarily a forest litter specialist; sampling on Table Mountain supports forest bias (J. Pryke, unpublished data): young forest (5.5/trap), natural forest (2.2/trap), riverine forest (1.7/trap), also in nearby pine plantation (1.8/trap) plus fynbos, regenerating fynbos and cultivated gardens (all 1/trap).
Food types: No quantitative assessment; type series recorded in humus; sampled using pig dung.
Temporal activity: Flightless; diel periodicity not recorded; sampled in spring, early summer and autumn (July to Jan., Apr.).
Bioregions South Africa: Centred on the most westerly extent of Southern Afrotemperate Forest (FOz 1) patches from which most samples were recorded.
Assessment rationale: EOO ~25 km^2, known AOO ~3 km^2 (area of FOz 1 on E slopes and ravines of Table Mountain); assumed to be originally associated with FOz 1 forest patches like its congener, *B. subtilis* (Boheman, 1857); owing to small EOO and even smaller AOO within the municipal boundaries of a major city, assessed as Vulnerable (VU), even though most known localities occur within a national park and some recent records originate from transformed habitats.
Conservation measures: Continuing protection of forest patches in Cape Town is probably essential for the conservation of this species despite some records from transformed habitats where it occurs at lower population density; protected within Table Mountain National Park.



Bohepilissus subtilis

(Boheman, 1857)

No synonyms

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Epilissus subtilis*: 'Caffraria meridionali' [inexact, probably S South Africa, possibly near Port Elizabeth].

Taxonomy: Accepted species, but may comprise a species complex owing to variation in setae, punctation, eye shape and aedeagi; this is represented as a geographical mosaic rather than a cline.

Distribution: S coastal region of Western and Eastern Cape with outliers on the NE coast of the Eastern Cape, South Africa.

Locality data (mean ± SD, range): Altitude: 422 ± 479, 0–1 993 m; annual rainfall: 492 ± 130, 356–961 mm; annual temperature (max. + min. /2): 16.2 ± 2.3, 9.6–19.7°C (N=29).

Habitat: No quantitative assessment; many records from relict patches of forest.

Food types: No quantitative assessment; mostly sifted from forest litter; also sampled to dung and carrion.

Temporal activity: Flightless; diel periodicity unknown; recorded in spring to early summer and autumn (Aug. to Mar.) reflecting seasonal rainfall of the bimodal rainfall region in the centre of its range.

Bioregions South Africa: Primarily in Southern Afrotemperate Forest (FOz 1) patches on the S coast and coastal mountains; outliers in Scarp Forest to the NE (FOz 5) (Forest Biome).

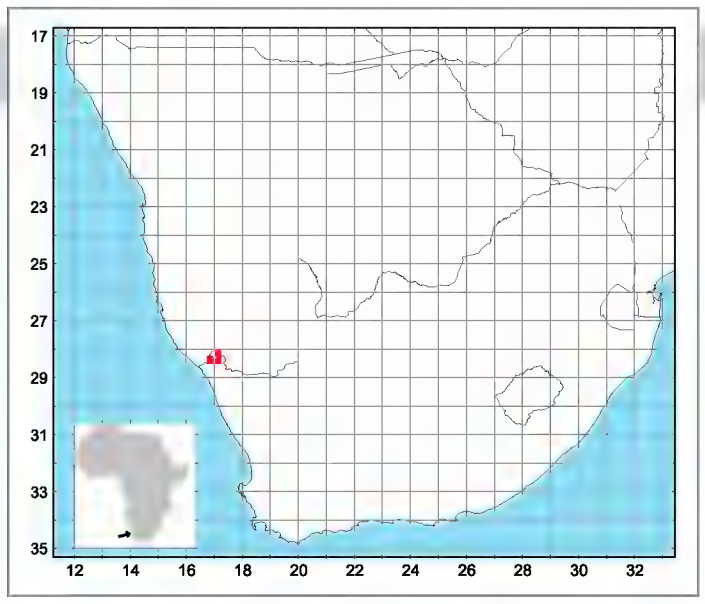
Assessment rationale: EOO = 38 100 km^2; assuming that *B. subtilis* represents a single variable species that differs between most neighbouring localities, it would not currently be seriously threatened as it is widespread and occurs in rather more than 10 separate locations, many of which are now protected within a national park; an unknown proportion of FOz 1 has been cleared in the past; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; however, continuing protection of FOz 1 forest patches would presumably be essential for the conservation of this species and its varieties; protected in the Garden Route National Park.

Genus *Byrrhidium* Harold, 1869

Type species and designation: *Byrrhidium ovale* Harold, 1869a, by subsequent designation (Janssens, 1938).
Synonyms: = *Elassocanthon* Kolbe, 1908: Type species: *Elassocanthon brevipes* Kolbe, 1908, by monotypy.
Last review: Entire genus reviewed by Scholtz and Howden (1987); synonymy of two species Deschodt et al. (2016).

Following the revision of Scholtz and Howden (1987) and the recent synonymy of two species (Deschodt et al. 2016), *Byrrhidium* Harold, 1869, is now reduced from three to just two species restricted to arid areas of Namaqualand in South Africa. Conservation of this genus may be dependent on persistence of concentrations of dung at hyrax middens or near refuges for rodents. However, this possibility needs to be tested.



Byrrhidium convexum

Scholtz & Howden, 1987

No synonyms

Global: DD (see IUCN Red List – DD)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Nunies/Sendelingsdrift at 28°18'S, 16°58'E' [South Africa on Namibian border].
Taxonomy: Accepted species.
Distribution: Extremely arid mountains of the Richtersveld, Northern Cape, in the arid north of the winter rainfall region, NW South Africa.
Locality data (mean ± SD, range): Altitude: 452 ± 187, 167–732 m; annual rainfall: 57 ± 11, 42–74 mm; annual temperature (max. + min. /2): 16.6 ± 0.7, 15.6–17.9°C (N=7).
Habitat: Sampled on sandy loam amongst shrubs and boulders of a rocky outcrop.
Food types: Sampled close to hyrax middens using pig dung bait.
Temporal activity: Flightless; diel periodicity unknown; recorded during spring (Oct., Nov.) and autumn (Apr.).
Bioregions South Africa: Vegetation unit: N tip of Central Richtersveld Mountain Shrubland (SKr 1) (Richtersveld, Succulent Karoo Biome); peripheral records in mountain or hilly vegetation units of the Desert Biome (Dg 2, Dg 3: inland Gariep Desert Bioregion; Dn 5: coastal Namib Desert Bioregion).
Assessment rationale: EOO = 163 km^2; poorly known with just a few qualitative observations of ecological associations; would qualify for an IUCN threat category on the basis of small known range at few locations; however, all but one of these known localities lie within a protected area; currently assessed as Data Deficient (DD).
Conservation measures: To assess conservation status, a quantitative survey of the Richtersveld is required to determine the full EOO, AOO and ecological associations; protected in Richtersveld National Park.

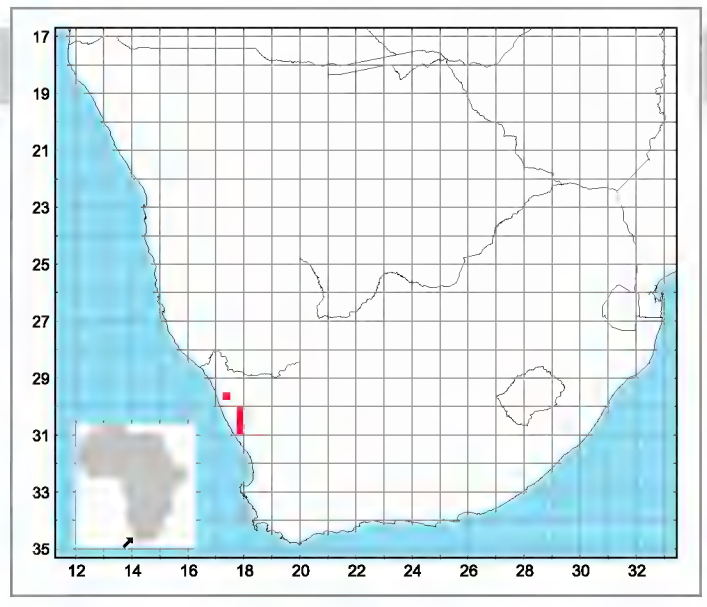
Byrrhidium ovale

Harold, 1869a

= *Elassocanthon brevipes* Kolbe, 1908
= *Byrrhidium namaquensis* Scholtz & Howden, 1987

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: *B. ovale*: 'Port Natal' [Durban, KwaZulu-Natal, South Africa; undoubtedly a locality error for this species, currently known only from Namaqualand]; *E. brevipes*: 'Klein-Namaland: Kamaggas' [Kommaggas, Namaqualand, South Africa]; *B. namaquensis*: 'Garies, Namaqualand' [South Africa].

Taxonomy: Accepted species.

Distribution: Arid regions above and below the W escarpment: Central to S Namaqualand, in the winter rainfall region of South Africa; citation for *B. ovale* from Namibia represents confusion over the location of 'Kamaggas' (*E. brevipes* type locality), which is situated in Little Namaqualand, South Africa, NOT Great Namaqualand in Namibia.

Locality data (mean ± SD, range): Altitude: 689 ± 373, 298–1 179 m; annual rainfall: 143 ± 25, 98–163 mm; annual temperature (max. + min. /2): 16.8 ± 1.2, 15.2–18.7°C (N=6).

Habitat: Sampled on sandy loam in relatively undisturbed shrubland with greater observed frequency close to *heuweltjies* (fossil termite mounds) inhabited by small mammals.

Food types: Sampled to pig dung, but possibly supported primarily by dung of small mammals inhabiting *heuweltjies*.

Temporal activity: Flightless, diel periodicity uncertain; either active in late afternoon, during darkness, or in early morning; recorded during the winter rainy season (July to Sept.); sampled under cool temperatures after rainfall in spring.

Bioregions South Africa: Vegetation unit: NW Namaqualand Klipkoppe Shrubland (SKn 1) (Namaqualand Hardeveld Bioregion, Succulent Karoo Biome).

Assessment rationale: EOO = 2 370 km^2; poorly known with ecological data supported only by qualitative observations; frequency apparently lower in disturbed habitat (e.g. overgrazing); probably deserves an IUCN threat category of at least Vulnerable (VU) on the basis of small range, < 10 known localities and probable sensitivity to grazing pressure; however, currently assessed as Data Deficient (DD).

Conservation measures: To adequately assess conservation status, a quantitative survey is required to document the full EOO, AOO and ecological associations, particularly bias to *heuweltjies* and possible effects of overgrazing and habitat disturbance; a small portion of the SKn 1 vegetation unit (4%) is protected in Namaqua National Park.

Genus *Chalconotus* Dejean, 1833

Type species and designation: *Scarabaeus cupreus* Fabricius, 1775, by monotypy.
Synonyms: = *Anachalcos* Hope, 1837: Type species: *Scarabaeus cupreus* Fabricius, 1775, by monotypy.
Last review: Entire genus reviewed as *Anachalcos* Hope, 1837, by Janssens (1938a); new species of *Anachalcos* added by Müller (1942), Josso and Prévost (2001).

Chalconotus Dejean, 1833, was recently revalidated as the senior generic name for species long classified in the genus, *Anachalcos* Hope, 1837 (Branco 2011). The large-bodied genus is endemic and widely represented in savannas and forest of the Afrotropical region where it is represented by nine species, all but one of which show intertropical distributions. The one exception that is also represented in southern Africa shows a pan-dry savanna distribution S of the Sahara and is, therefore, assessed as Least Concern (LC).

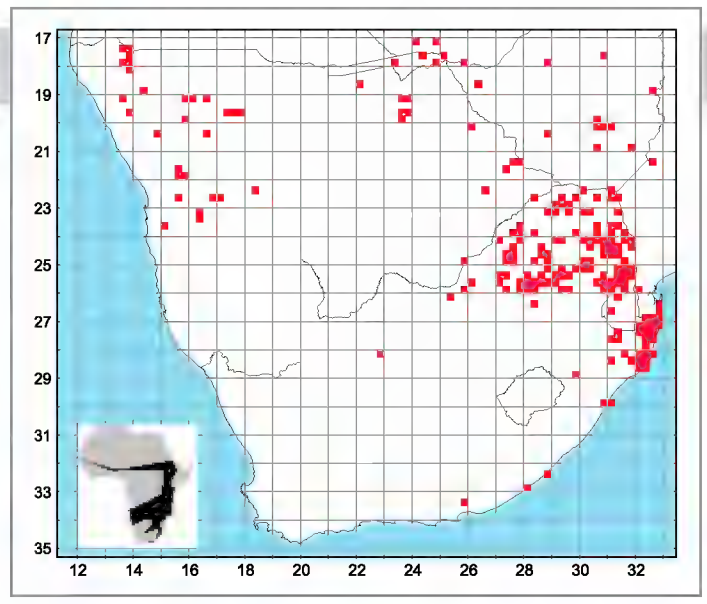
Chalconotus convexus

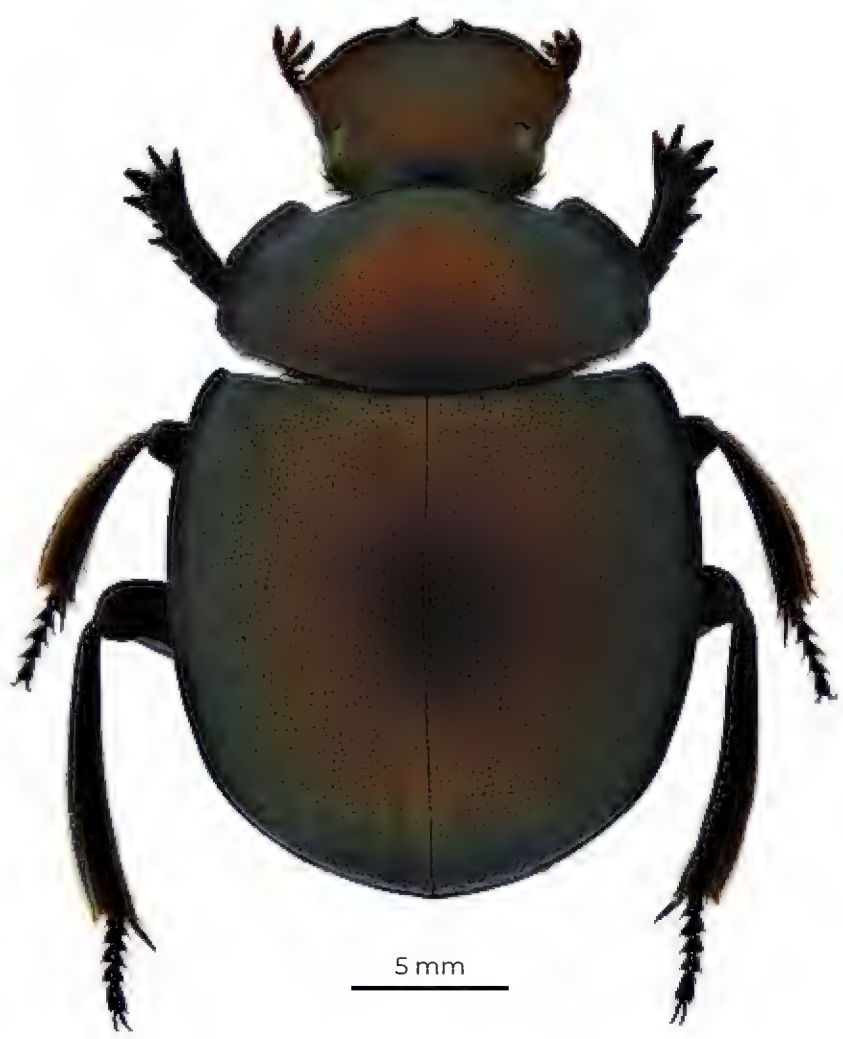
Boheman, 1857

= *Anachalcos obscurus* van Lansberge, 1882
= *Anachalcos sericeus* Felsche, 1907

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J





Type localities: *C. convexus*: 'Caffraria interior' [inexact, interior of South Africa]. *A. obscurus*: 'Somalis (Afrique Équatoriale)' [inexact, Somalia]; *A. sericeus*: 'Kionga' [Quionga, N Mozambique].

Taxonomy: Accepted species; recently transferred to *Chalconotus* Dejean, 1833, from *Anachalcos* Hope, 1837.

Distribution: Widespread in drier savanna, S to E to W Africa: South Africa, Mozambique, Zimbabwe, Botswana, Namibia, Angola, Kenya, Tanzania, Somalia, Nigeria; also reported from Malawi, Democratic Republic of the Congo, Uganda, Ethiopia, Eritrea, Benin, Côte d'Ivoire, Burkina Faso, Senegal.

Locality data (mean ± SD, range): Altitude: 790 ± 509, 0–1 850 m; annual rainfall: 646 ± 191, 22–1 254 mm; annual temperature (max. + min. /2): 20.3 ± 2.3, 13.4–25.9°C (N=335).

Habitat: In Gauteng bushveld: bias to finer-grained soils, sandy clay loam (346), deep sand (110); in uMkhuze Game Reserve: more equitable distribution, deep sand (13.8), sand over clay (22.2), sandy clay loam (15.8), clay (7.7); in Gauteng bushveld: strong bias to shaded thickets (270), open woodland (167), grassland (19); largely supported by DBRU collection records: sand (10), sandy loam (5), sandy clay loam (7), clay (4) in forest (16), open shrub/woodland (19) and grassland/pasture (5).

Food types: In Gauteng bushveld: readily attracted to cattle dung in habitat sampling, but quantitative trophic sampling shows extreme bias to carrion (60) and omnivore dung (pig: 112) compared to herbivore dung (horse: 1, cattle: 4); not so extreme at Phalaborwa: dung of pig (542), elephant (108), cattle (36); DBRU collection records on dung: mixed human/cattle or buffalo (13), elephant (13), rhinoceros (2), horse (1), cattle (9), wildebeest (1).

Temporal activity: Flight activity in darkness, but also observed constructing cattle dung balls in early morning light following rainfall; in Gauteng bushveld: active during the summer rainy season with peak activity in early to mid-summer (Oct. to Feb.) tailing off into late summer (Mar. to Apr.); also spring activity (Aug.) at the warmer KwaZulu-Natal coastline; at Phalaborwa: abundant activity in warm weather after light rain (185), heavy rain (302) or in dry conditions (202); attracted to light.

Ecoregions Namibia, Botswana, Zimbabwe: Centred on Southern African Bushveld (AT0717), Zambezian and Mopane Woodlands (AT0725), Southern Miombo Woodlands (AT0719), Namibian Savanna Woodlands (AT131), Angolan Mopane Woodlands (AT0702); E and W separated by deep Kalahari sand ecoregions.

Bioregions South Africa: Primarily Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl); also Sub-Escarpment Savanna (SVs) (Savanna Biome), Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 6 750 790 km^2 (gross estimate); although bias to shaded and woody habitats suggest that local clearance of woodland would be a threat, it would be little threatened over most of its extremely widespread range throughout drier savanna of Africa where it readily colonises cattle dung despite bias to omnivore dung and carrion; assessed as Least Concern (LC).

Conservation measures: None required; protected in various national parks and game reserves, including Kruger (South Africa), Etosha (Namibia), Lake Mutirikwe (Zimbabwe), Tsavo West (Kenya), Yankari (Nigeria).

Genus *Circellium* Latreille, 1829

Type species and designation: *Scarabaeus bacchus* Fabricius, 1781, by monotypy.
Synonyms: None.
Last review: Entire genus reviewed by Scholtz and Howden (1987).

Usually cited as *Circellium* Latreille, 1825 but first listing as '*Circellie*' is in Latreille, 1829. *Circellium* Latreille, 1829 is very large bodied, flightless and monotypic with a patchy distribution restricted to the S coast of South Africa. It is assessed as Vulnerable (VU) owing to its flightless condition and high levels of disturbance over much of its range. Nevertheless, despite patchy and mostly uncommon occurrence along the S Cape coastal regions, it occurs with high frequency in the least disturbed, sandy, shrubland areas of Addo Elephant National Park.

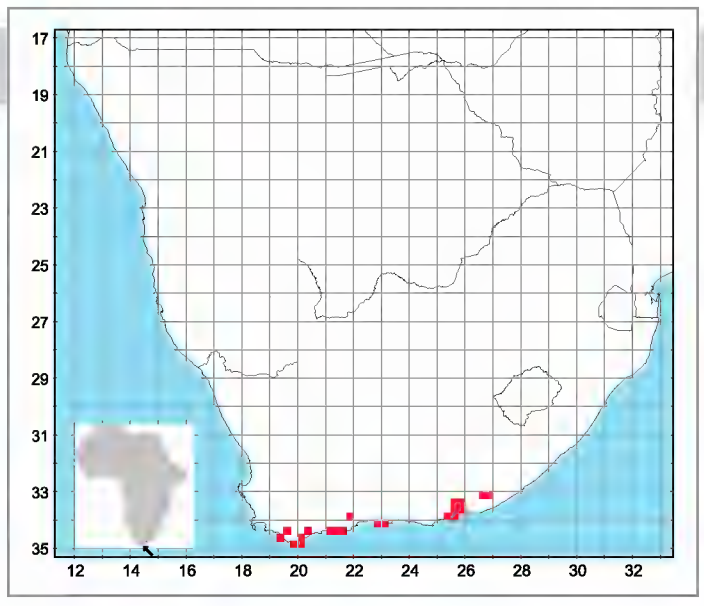
Circellium bacchus

(Fabricius, 1781)

= *Scarabaeus hemisphaericus* Pallas, 1781
= *Circellium lyceus* Westwood, 1837a
= *Circellium bacchus* var. *waterhousei* Shipp, 1895a

Global: VU
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: As *Scarabaeus bacchus*: 'Cap bon. sp.' [Cape of Good Hope, South Africa]; *S. hemisphaericus*: Not stated; *C. lyceus*: 'Sierra Leone' [undoubtedly an erroneous locality]; *C. bacchus* var. *waterhousei*: 'Matabili-land' [Matabeleland, SW Zimbabwe; considered a most doubtful locality].

Taxonomy: Accepted species.

Distribution: Centred on the S coastline, South Africa, in the winter and bimodal rainfall regions; E and W populations are genetically distinct, presumably, due to disjunction after Pliocene sea level rise; published records from NE South Africa, Namibia, Zimbabwe, Mozambique, Tanzania and Sierra Leone are considered to be errors; claims for range contraction, linked to that of hooked-lipped (black) rhinoceros and their dung, are not supported by food type associations.

Locality data (mean ± SD, range): Altitude: 151 ± 146, 0–535 m; annual rainfall: 431 ± 42, 346–531 mm; annual temperature (max. + min. /2): 17.2 ± 0.9, 14.9–18.7°C (N=24).

Habitat: No quantitative assessment of soil type association; in Addo Elephant National Park: abundant in dense shrub/woodland on sandy soils; most uncommon in adjacent disturbed open vegetation.

Food types: In Addo Elephant National Park: elephant dung preferred for feeding, buffalo and cattle dung for breeding; also recorded on dung of monkey, human, rhinoceros, hare, ostrich.

Temporal activity: Flightless, ectothermic and diurnal with maximal activity between 18–26°C, particularly after rainfall; recorded in every month of the year, but low abundance in autumn and winter (Apr. to July); female makes and rolls balls of dung for brood construction, which is done by males in many other species.

Bioregions South Africa: E populations: Albany Thicket Biome (AT); W populations: vegetation units in Shale Renosterveld (FRs), Limestone Fynbos (FFl), Sandstone Fynbos (FFs), Sand Fynbos (FFd), Strandveld (FS) (Fynbos Biome).

Assessment rationale: EOO = 11 950 km^2; AOO would be smaller as much of the mapped range falls within or borders vegetation units in which the natural vegetation is threatened (transformation: AT: 1.5–35%, FS: 5–50%, FR: 58–61%, FF: 17–70%); this is a cause for concern as clearance of natural shrubland results in a radical decline in population density whereas range fragmentation is exacerbated by low vagility due to flightlessness; only 5% of the range is protected within natural shrubland reserves, mostly comprising small fragments; it has the distinction of being the only South African dung beetle specifically protected by law (Proclamation 24/1992 – Western and Eastern Cape Provinces).

Conservation measures: E populations are abundant in the relatively large Addo Elephant National Park (1 640 km^2) where elephant and buffalo dung is common; however, rangers report that traffic road kill is a problem in Addo where dung from elephants is common on roads that are used for ease of passage through dense shrubland; even so, genetic subunits of W populations might be more vulnerable as they are only protected in various small nature reserves, including De Hoop, Goukamma, Salmonsdam.

Genus *Dicranocara* Frolov & Scholtz, 2003b

Type species and designation: *Dicranocara deschodti* Frolov & Scholtz, 2003b, by original designation.
Synonyms: None.
Last review: All species reviewed by Deschodt and Scholtz (2007); one species added by Moretto (2016).

The flightless genus, *Dicranocara* Frolov & Scholtz, 2003b, is entirely restricted to rocky river valleys and mountains just to the N and S of the lower Orange River where it has been recorded close to rock hyrax middens. Although a new species has now been described from the rocky edges of the upper Fish River, no *Dicranocara* species were recorded during a survey along the lower Fish River that is bordered by sand and lacked hyrax colonies.

All species appear to occupy very small ranges where they may be supported mainly by concentrations of dung in hyrax middens, which currently represent an assured dung supply. Although the ranges of three species lie entirely within protected areas, one of these areas has now been granted as a mining concession so that the assessment for that species has been changed from Least Concern (LC) to Vulnerable (VU).

Dicranocara deschodti

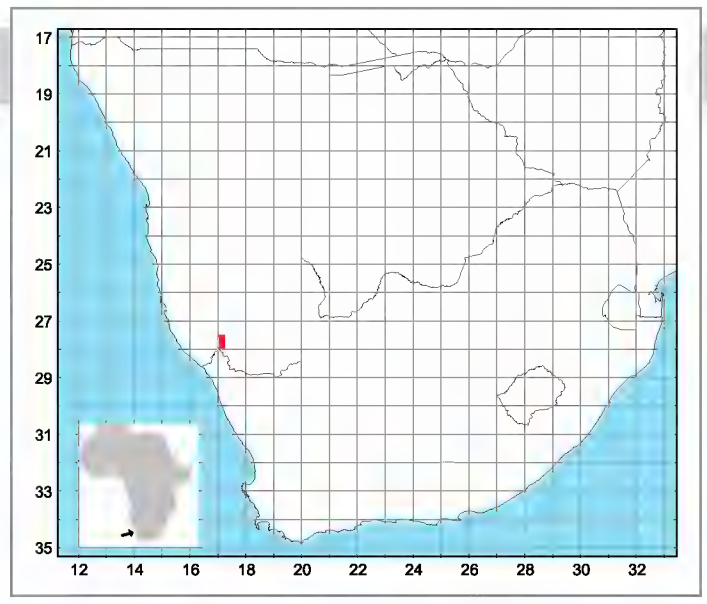
Frolov & Scholtz, 2003b

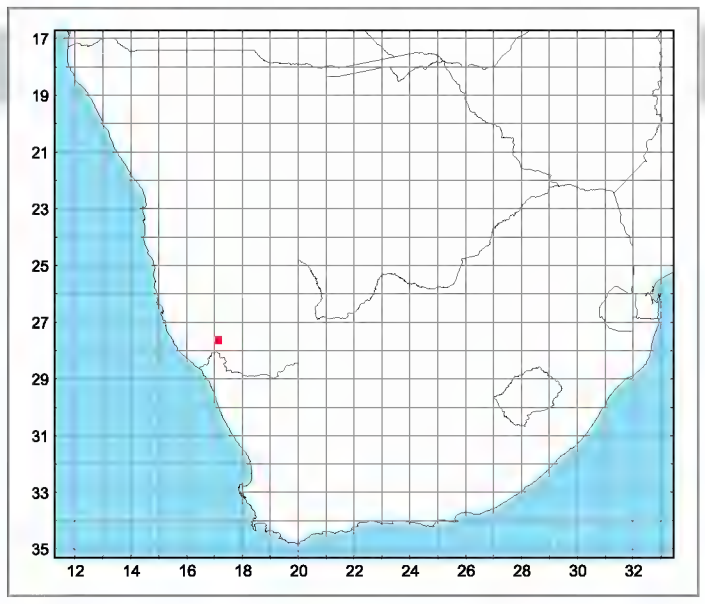
No synonyms

Global: VU (see IUCN Red List – LC)
Endemic: Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Namibia, Boom River, 27°59'S 17°03'E'.
Taxonomy: Accepted species; sexually dimorphic (head); prominence of characters varies with body size.
Distribution: Only known from the Boom River Valley; probably endemic to this usually dry, S Namibian river system that drains southwards into the lower Orange River; nearby rocky-edged tributaries are occupied by other species.
Locality data (mean ± SD, range): Altitude: 769 ± 243, 339–930 m; annual rainfall: 81 ± 19, 50–99 mm; annual temperature (max. + min. /2): 16.5 ± 0.9, 15.9–17.9°C (N=5).
Habitat: Accumulations of sand at the bases of mountains and rocks bordering the river bank near rock hyrax colonies.
Food types: Associated with piles of dung pellets contained in or near communal hyrax middens; mouthparts modified, probably for the use of dry food.
Temporal activity: Flightless, active in darkness; uses the clypeal projections at the front of the head to transport hyrax pellets; these are carried across rocks and buried in the soil at the base where a single breeding mass of dung containing an egg is constructed at the end of a short tunnel.
Ecoregions Namibia: Near the NW tip of the Nama Karoo (AT1314).
Assessment rationale: EOO = 190 km^2; despite flightless condition and small known EOO, formerly assessed as Least Concern (LC) since its range occurs entirely within a protected area where it would probably not face current threats as long as a supply of dung is maintained, which seemed relatively assured given the widespread occurrence of the rock hyrax in arid regions; however, the entire known range in the Boom River Valley has now been granted as a diamond mining concession and access has been barred in terms of the Diamond Act of 1999; as disturbance by mining could impact on its habitat and the density of hyrax colonies, the assessment has been revised to Vulnerable (VU).
Conservation measures: Although protected within the Ai-Aïs/Richtersveld Transfrontier Park, granting of the entire known EOO as a mining concession means that impact of mining activities will need to be assessed at a later date.





Dicranocara inexpectata

Deschodt & Scholtz, 2007

No synonyms

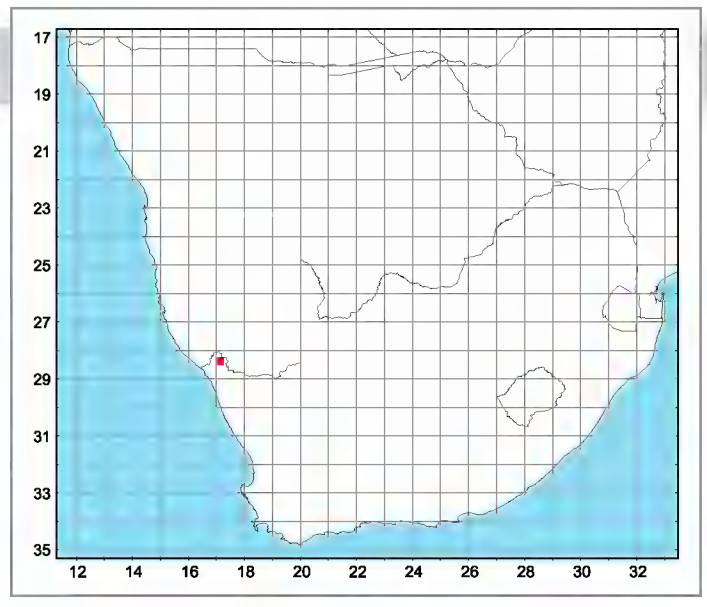
Global: DD
Endemic: Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Richtersveld, Witputs RD' [S Namibia].
Taxonomy: Accepted species; sexually dimorphic (head), characters vary in prominence with body size.
Distribution: Possibly highly localised within an area to the N of the source of the Boom River, the Boom River Valley lies 45 km to the S and forms the type locality of *D. deschodti* Frolov & Scholtz.
Locality data (average): Altitude: 867 m; annual rainfall: 99 mm; annual temperature (max. + min. /2): 16.9°C (N=1).
Habitat: No quantitative assessment; type series recorded on a small boulder-strewn outcrop.
Food types: No quantitative assessment; type series collected around hyrax middens.
Temporal activity: Flightless; diel periodicity unknown, but presumably active in darkness like *D. deschodti*; recorded during the late summer rainy season (Mar., Apr.).
Ecoregions Namibia: Near the NW tip of the Nama Karoo (AT1314).
Assessment rationale: EOO unknown; probably not threatened as the area is used primarily for grazing domestic livestock, but it would qualify for an IUCN threat category if the EOO proves to be very small; currently assessed as Data Deficient (DD).
Conservation measures: To assess conservation status, a quantitative survey is required to determine the EOO and AOO, also to confirm the observed ecological associations; known only from the type locality, which lies outside of protected areas.

Dicranocara tatasensis

Deschodt & Scholtz, 2007

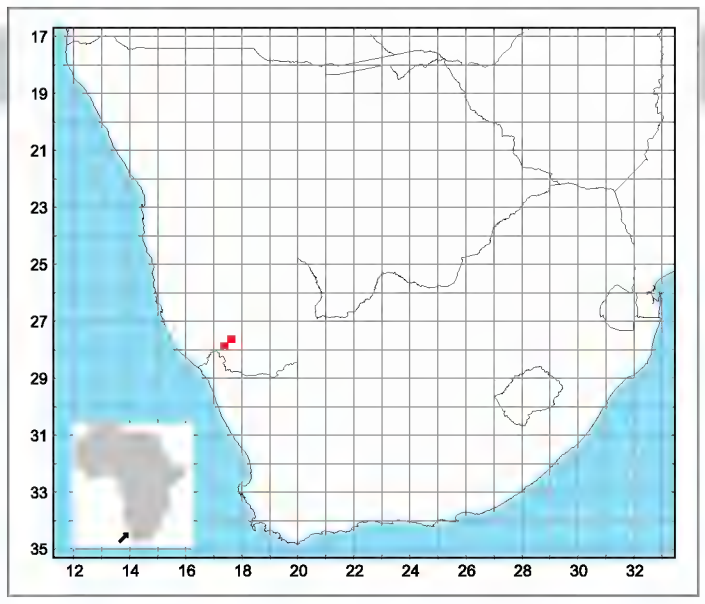


No synonyms

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Tatasberg, Richtersveld Nat. Park' [NW South Africa].
Taxonomy: Accepted species; sexually dimorphic (head), characters vary in prominence with body size.
Distribution: Known only by the type series collected in higher parts of the Tatasberg at the S edge of the lower Orange River Valley, South Africa.
Locality data (average): Altitude: 372 m; annual rainfall: 53 mm; annual temperature (max. + min. /2): 17.7°C (N=1).
Habitat: No quantitative assessment; type series collected dead or alive amongst boulders close to hyrax middens in a vegetation unit characterised by sandy loam and scrub.
Food types: No quantitative assessment; probably primarily hyrax dung pellets.
Temporal activity: Flightless; diel periodicity unknown, but presumably active in darkness like *D. deschodti* Frolov & Scholtz, 2003; recorded during the late summer rainy season (Mar., Apr.).
Bioregions South Africa: Vegetation unit: Tatasberg Mountain Succulent Shrubland (SKr 9) (Richtersveld Bioregion, Succulent Karoo Biome).
Assessment rationale: EOO = 3.3 km² (based on area of SKr 9); known only from a very small upland island of Succulent Karoo vegetation; SKr 9 is entirely isolated in the Gariep Desert Bioregion of the Desert Biome; despite a possibly minute range it was found close to a relatively assured food supply; also, the entire range occurs within a protected area; therefore, currently assessed as Least Concern (LC) although it has been described as rare and would be vulnerable to decline in hyrax population density.
Conservation measures: A survey is required to confirm that this species is restricted to the Tatasberg and does not occur in the slightly moister desert mountains to the S; if so, conservation status might require revision on the basis of small range at a single location; protected in the Richtersveld National Park (South Africa).



Dicranocara vandersmisseni

Moretto, 2016a

No synonyms

Global: DD
Endemic: Namibia

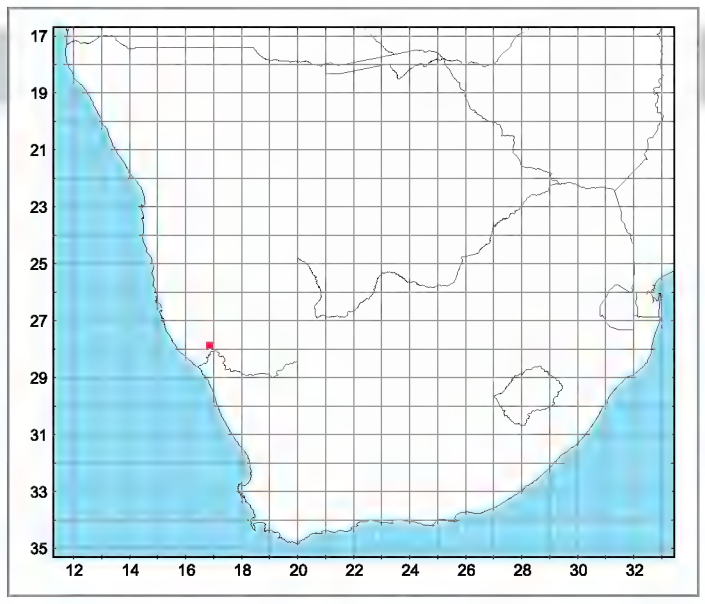
J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Namibie, Karas, Ai-Aïs' [Ai-Aïs, S Namibia].
Taxonomy: Accepted species; sexually dimorphic (head), characters vary in prominence with body size.
Distribution: Known only by the type series of three individuals collected along those parts of the Fish River that are bordered by rocky edges, which support hyrax colonies.
Locality data (mean ± SD, range): Altitude: 449 ± 138, 351–547 m; annual rainfall: 91 ± 44, 60–122 mm; annual temperature (max. + min. /2): 19.6 ± 0.1, 19.5–19.7°C (N=2).
Habitat: No quantitative assessment; soil and vegetation associations unknown.
Food types: No quantitative assessment; probably, primarily hyrax dung pellets; one individual found dead in a hyrax midden (Aug.).
Temporal activity: Flightless; diel periodicity unknown, but possibly active in darkness like *D. deschodti* Frolov & Scholtz, 2003; recorded alive in the soil in mid-summer (Jan.); dead specimens recorded in spring and mid-summer (Aug., Jan.).
Ecoregions Namibia: NW edge, Nama Karoo (AT1314).
Assessment rationale: EOO = 300 km^2; ecologically very poorly known; therefore, currently assessed as Data Deficient (DD); however, assumed to be associated primarily with hyrax middens, and would therefore be vulnerable to decline in hyrax population density.
Conservation measures: A survey is required to confirm that this species is restricted to rocky areas of the arid Fish River Valley; protected within the borders of the Ai-Aïs/Richtersveld Transfrontier Park.

Genus *Drogo* Deschodt, Davis & Scholtz, 2016

Type species and designation: *Drogo stalsi* Deschodt, Davis & Scholtz, 2016, by original designation.
Synonyms: None.
Last review: Genus created by Deschodt et al. (2016).

Drogo Deschodt, Davis & Scholtz, 2016, is a flightless, monotypic genus that is known only from the type locality in mountains just N of the lower Orange River in Namibia. The genus has been recorded only in farm rangeland although habitat disturbance is, apparently, limited.



Drogo stalsi

Deschodt, Davis & Scholtz, 2016

No synonyms

Global: DD
Endemic: Namibia

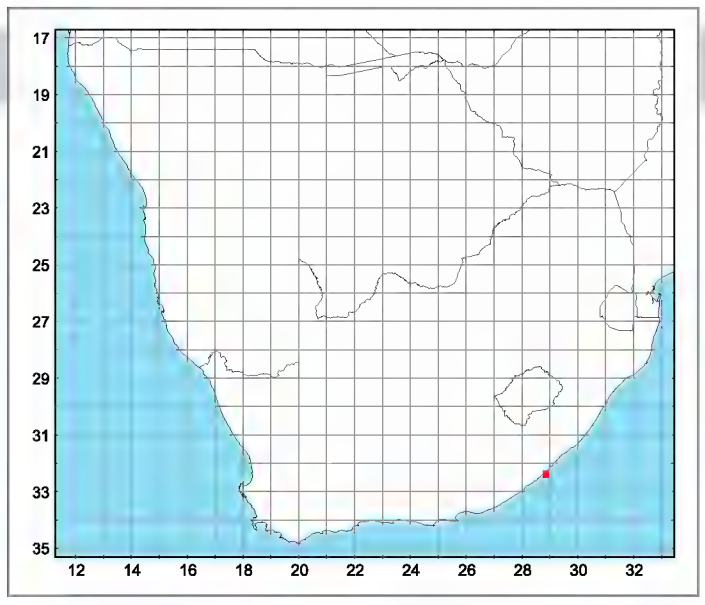
J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Zebrafontein, ± 30 km, NNE of Rosh Pinah' [Farm in S Namibia].
Taxonomy: Accepted species; known only by the male holotype.
Distribution: Known only from the type locality in arid S Namibia just N of the Orange River.
Locality data (average): Altitude: 1 608 m; annual rainfall: 123 mm; annual temperature (max. + min. /2): 12.9°C (N=1).
Habitat: Unknown.
Food types: Unknown.
Temporal activity: Flightless, diel periodicity unknown; recorded during the late summer rainy season (Apr.).
Ecoregions Namibia: NW edge, Nama Karoo (AT1314).
Assessment rationale: EOO unknown; known only by the male holotype; arid type locality unprotected, not apparently heavily disturbed although used for the grazing of domestic livestock; unclear if *D. stalsi* faces any threats; assessed as Data Deficient (DD) since so little is known about the species.
Conservation measures: To adequately assess conservation status, a quantitative survey is required to document the full EOO, AOO and ecological associations; the type locality falls outside of and between the boundaries of Sperrgebiet and Richtersveld National Parks.

Genus *Dwesasilvasedis* Deschodt & Scholtz, 2008

Type species and designation: *Dwesasilvasedis medinae* Deschodt & Scholtz, 2008, by original designation.
Synonyms: None.
Last review: Genus created by Deschodt and Scholtz (2008).

Dwesasilvasedis Deschodt & Scholtz, 2008, is flightless, small-bodied and monotypic; known only from leaf litter in a single small patch of forest on the SE coast of South Africa. By virtue of its habits and small range in a single known location, it is assessed as Vulnerable (VU).



Dwesasilvasedis medinae

Deschodt & Scholtz, 2008

No synonyms

Global: VU
Endemic: RSA

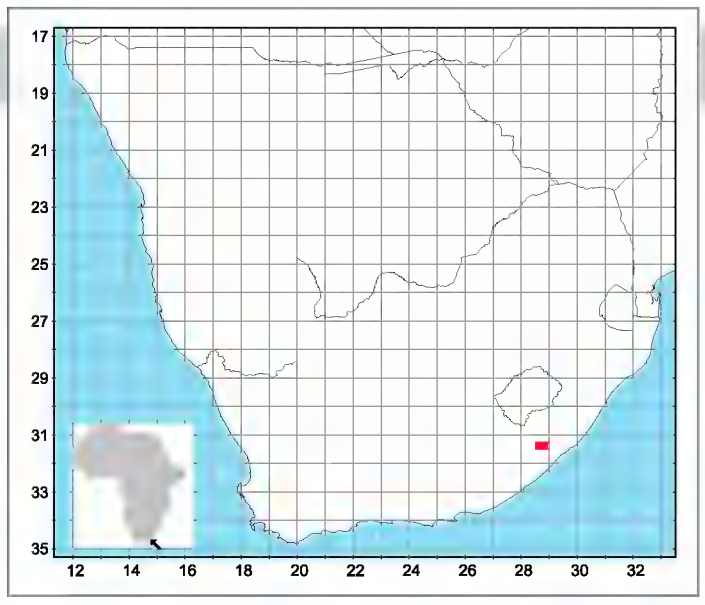
J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Dwesa Forest, Eastern Cape' [South Africa].
Taxonomy: Accepted species; sexually dimorphic (head).
Distribution: Known only from the type locality of Dwesa Forest.
Locality data (average): Altitude: 112 m; annual rainfall: 899 mm; annual temperature (max. + min. /2): 18.9°C (N=1).
Habitat: No quantitative assessment; all specimens in type series (19) sifted from leaf litter in indigenous forest in an area dominated by sandy loam soils; assumed to be a forest specialist.
Food types: Not known.
Temporal activity: Diel periodicity not known; recorded in the summer rainy season (Nov.).
Bioregions South Africa: Scarp Forest (FOz 5) (Forest Biome).
Assessment rationale: EOO = 28.6 km² (area of Dwesa Forest); almost contiguous with adjoining Cwebe Forest (18.4 km²); Dwesa-Cwebe Forest is an isolated patch of Transkei Coastal Scarp Forest; it is unknown whether or not this species occurs in other much smaller patches of FOz 5 to the S and N; although officially protected as the Dwesa-Cwebe Wildlife Reserve, it is utilised for cutting of poles and hunting; owing to small known range in few locations that are under exploitation pressure *D. medinae* is assessed as Vulnerable (VU).
Conservation measures: Continuing protection of indigenous forest in Dwesa-Cwebe Wildlife Reserve would be essential for the conservation of this monotypic genus; a survey of other nearby FOz 5 Scarp Forest patches to N and S would provide a better supported assessment of EOO and conservation status; vegetation specialisation and AOO should be confirmed by a gradsect across the forest edge.

Genus *Endroedyolus* Scholtz & Howden, 1987

Type species and designation: *Endroedyolus paradoxus* Scholtz & Howden, 1987, by original designation.
Synonyms: None.
Last review: Genus created by Scholtz and Howden (1987).

Endroedyolus Scholtz & Howden, 1987, is small-bodied, flightless and monotypic. It has been recorded from leaf litter in a few small upland forest patches in the mistbelt of SE South Africa. Because of its flightless condition, very small known range and threats to its only two known locations, the genus has been assessed as Endangered (EN).



Endroedyolus paradoxus

Scholtz & Howden, 1987

No synonyms

Global: EN (See IUCN Red List – EN)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Transkei, Umtata, Nquadu Mt.' [Eastern Cape, South Africa]
Taxonomy: Accepted species.
Distribution: Forest patches on coastal hills in the vicinity of Mthatha, Eastern Cape, South Africa.
Locality data (mean ± SD, range): Altitude: 1 170 ± 61, 1 126–1 213 m; annual rainfall: 1 111 ± 136, 1 015–1 207 mm; annual temperature (max. + min. /2): 15.6 ± 0.4, 15.3–15.8°C (N=2).
Habitat: No quantitative assessment; recorded from only two indigenous forest localities.
Food types: No quantitative assessment; type series sifted from forest floor leaf litter; subsequently sampled using dung baits.
Temporal activity: Flightless; diel periodicity not known; recorded during the summer rainy season (Dec.).
Bioregions South Africa: Southern Mistbelt Forest (FOz 3) (Forest Biome).
Assessment rationale: EOO = 80 km^2; AOO = 8.9 km^2; EOO and AOO possibly underestimated as there is a group of > 20 isolated FOz 3 forest patches between Mthatha and Cala; however, this monotypic genus is currently known only from the type locality and one other nearby forest patch (Mhlanlane Forest Station) at the E end of these forest patches; assessed as Endangered (EN) in the IUCN Red List; both known localities are currently state-protected forests although Nqadu Forest is subject to a land claim; also past fires have destroyed much of the habitat and commercial plantations have replaced much of the native forest; even if future survey demonstrates a larger EOO, probably deserves at least Vulnerable (VU) status although somewhat Data Deficient (DD) at present.
Conservation measures: Protection of FOz 3 forest patches is essential for the conservation of this species, particularly Nqadu and Mhlanlane; to provide a more balanced assessment of EOO, a survey is required in forest patches between Umtata and Cala, and those to the S and N; a gradsect from grassland into forest patches would confirm the vegetation specialisation and restricted AOO; it would also generate data on population density and assist assessment of conservation status.

Genus *Epirinus* Dejean, 1833

Type species and designation: *Scarabaeus flagellatus* Fabricius, 1775, by subsequent designation (Ferreira, 1972 – earlier designations by Reiche, 1841 and Janssens 1938a ruled invalid by Daniel, 2019).

Synonyms: = *Endroedyantus* Cambefort, 1978; Type species: *Endroedyantus silvestris* Cambefort, 1978, by original designation.

Last review: All species reviewed by Scholtz and Howden (1987); new species, revised key and morphological phylogeny (Medina & Scholtz 2005); new species and synonymies (Deschodt et al. 2019) (see Preamble).

The long-established genus, *Epirinus* Dejean, 1833, comprised 29 species when the manuscript was completed at the end of 2017. Subsequently, Deschodt et al. (2019) have described five new species that are not included in the species accounts and have synonymised two others (see species accounts for *E. hluhluwensis*, *E. ngomae*, and Preamble). At the end of 2017, available data indicated that the genus was endemic to South Africa, Eswatini and Lesotho, but one recent record for *Epirinus flagellatus* (Fabricius, 1775) extends the range to N Namibia (Deschodt et al. 2019). Six species have been observed to roll balls of dung despite small body size.

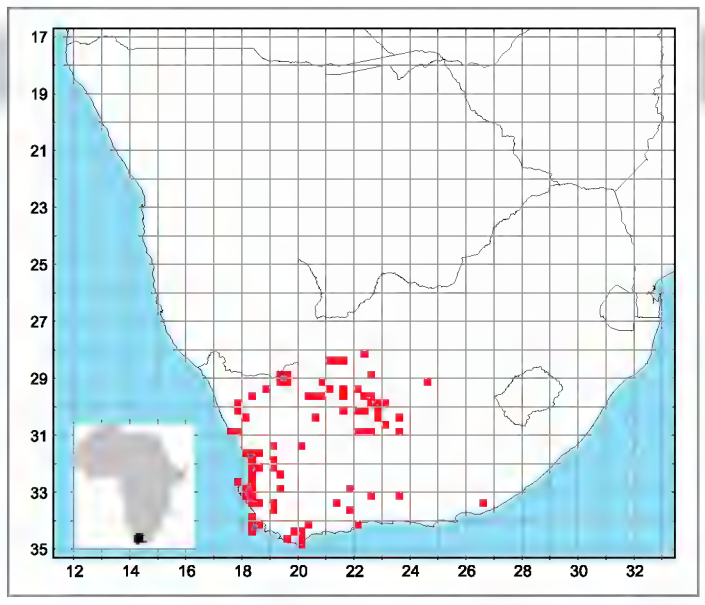
As there is some conflict between relationships defined by morphological (Medina & Scholtz 2005) and partial molecular phylogenies (Mlambo et al. 2015), it is uncertain how to define centres of distribution. However, the morphological phylogeny suggests a complex history of radiation and speciation along four main lineages with the most basally derived lineages containing species centred more to the SW and the most derived containing some species centred more to the NE. Species centred on cooler SW regions are primarily active during the winter rainy season from autumn to spring. Those centred on cooler uplands or forest patches to the NE are primarily active during the summer rainy season.

Flightless species (10, reduced to 8) are primarily centred on coastal and mountain forest patches along the S and E seaboard. Phylogenies variously divide them into two lineages centred to the SW or NE. All but one species show small EOOs from 81 to 2 300 km^2. Distributions are centred on the S Cape (3), E Cape (4) or NE KwaZulu-Natal (3 – now synonymised as a single species, *E. davisi* Scholtz & Howden, 1987).

Species centred primarily on moister E Highveld grasslands and S Cape fynbos (8) occur in two different lineages. Most show large EOOs although known ranges of a few are very small (80–170 km^2). Distributions are centred on NE Highveld (4, one in forest), E Highveld (1), NE Highveld to S Cape (2), S Cape (1).

The remaining 11 species show SW centres of distribution, but occur in three different lineages. Most show large EOOs other than those (4) on the SW coast and mountains (15–3 400 km^2). Distributions are centred on W (2) or SW (2) coastal sands, SW mountains (1), SW fynbos (1), SE shrubland and Highveld Grassland (1), W Highveld Grassland (1), Upper Karoo (1) or they are widespread primarily in SW fynbos and Karoo (2).

On the basis of widespread occurrence 11 species are assessed as Least Concern (LC) with the remainder assessed as Data Deficient (DD: 14) or Vulnerable (VU: 4). Many of the known distributions are relatively small, particularly those found in forest. Many are centred on or overlap into regions of high habitat transformation. It is probable that many of those assessed as DD would qualify for an IUCN threat category. Severely limited available data suggest that clearance of indigenous SW shrubland is detrimental to population density in three species. Disturbance in Highveld Grassland may also reduce population density. Only small parts of the ranges of most species are under protection.



Epirinus aeneus

(Wiedemann, 1823)

= *Epirhinus deplanatus* Boheman, 1858

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Canthon aeneus*: 'Prom. bon. sp.'; *E. deplanatus*: 'Promontorium Bonae Spei' [both, Cape of Good Hope, South Africa].
Taxonomy: Accepted species.
Distribution: Widespread in the Nama Karoo and the winter and bimodal rainfall regions of South Africa comprising Fynbos and Succulent Karoo.
Locality data (mean ± SD, range): Altitude: 652 ± 466, 0–1 614 m; annual rainfall: 231 ± 94, 66–539 mm; annual temperature (max. + min. /2): 17.6 ± 1.6, 12.4–21.7°C (N=125).
Habitat: In Western Cape: abundant in shrubland on deep sand (Modderrivier: 306; Pampoenvlei: 353) and pasture grassland cleared of shrubs on sandy loam (Oranjefontein: 159; Waylands: 258); on deep sand in West Coast National Park: less abundant in natural shrubland (320) than in sparse-grass pasture (607) resulting from shrubland clearance; DBRU collection records primarily from coarse-grained soils: sand (28), sandy loam (3), sandy clay loam (4) in scrub/shrubland (18), also pasture/grassland (7), fallow crop fields (6).
Food types: No quantitative data; DBRU collection records from cattle (31), buffalo (1), horse (4), sheep (1) dung.
Temporal activity: Diurnal flight; probably in sunshine as long as temperatures are suitable; in winter rainfall region of Western Cape: autumn, winter, spring activity by adults, sclerotised (Apr. to Oct.), teneral (Sept. to Nov.).
Bioregions South Africa: Known from all three bioregions of the Nama Karoo Biome; also S Namaqualand Sandveld (SKs), Namaqualand Hardeveld (SKn) and Rainshadow Valley Karoo (SKv) (Succulent Karoo Biome); as well as units of Fynbos (FF), Strandveld (FS) and Renosterveld (FR) (Fynbos Biome).
Assessment rationale: EOO = 335 500 km^2; widespread in both highly transformed regions in the SW Western Cape (25–80%; FF, FS, FR) and little-transformed regions used primarily for grazing of livestock in Namaqualand and the Nama Karoo; abundance in pastures cleared of natural shrubland and records from fallow crop fields suggest that habitat transformation is less detrimental to *E. aeneus* than to many other species with endemic SW distribution patterns; assessed as Least Concern (LC).
Conservation measures: Assessment of conservation status would be improved by further quantitative data on ecological associations; protected in Bontebok and West Coast national parks.

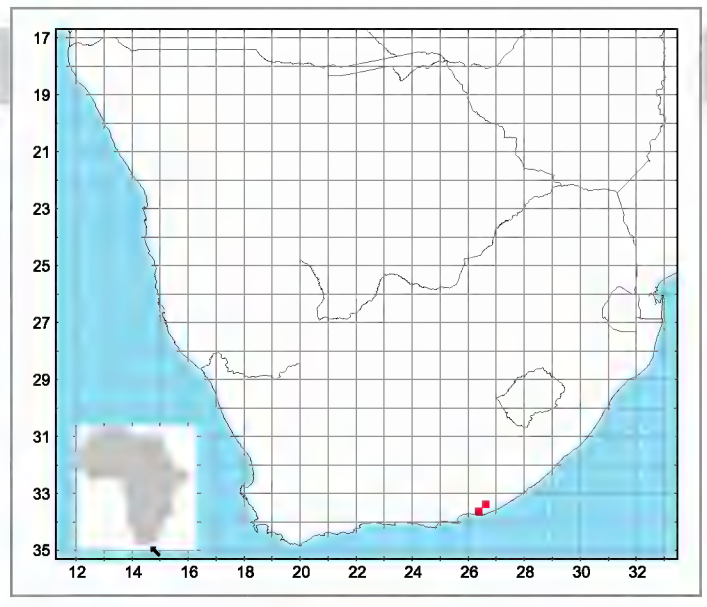
Epirinus aquilus

Medina & Scholtz, 2005

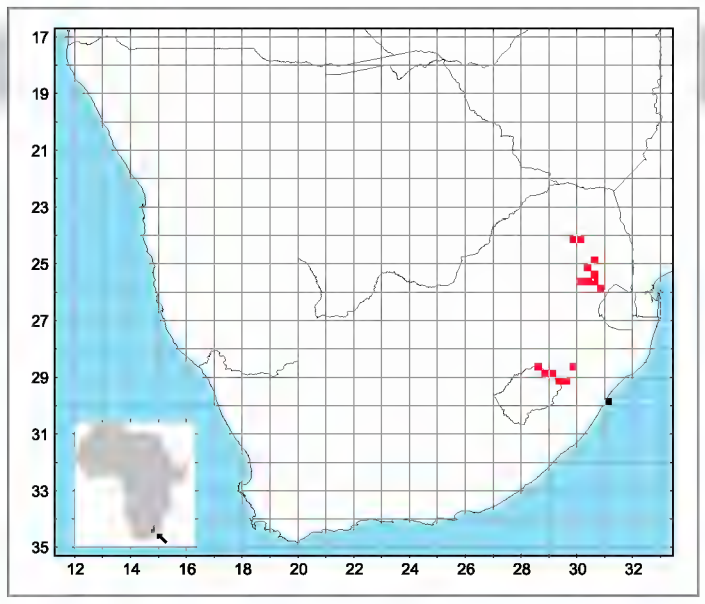
No synonyms

Global: VU
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: 'Grahamstown' [Eastern Cape, South Africa].
Taxonomy: Accepted species.
Distribution: Known only from the isolated coastal Alexandria State Forest and one other, nearby, hillside forest patch (holotype locality), close to Grahamstown, Eastern Cape, South Africa.
Locality data (mean ± SD, range): Altitude: 402 ± 394, 123–681 m; annual rainfall: 539 ± 80, 482–595 mm; annual temperature (max. + min. /2): 16.8 ± 1.3, 15.9–17.7°C (N=2).
Habitat: No quantitative assessment; recorded only in forest established on sandy soils; the coastal Alexandria Forest borders the Alexandria dune field.
Food types: No quantitative assessment; sampled to pig dung.
Temporal activity: Diurnal, flightless, primarily active in the summer rainy season (Jan. to May).
Bioregions South Africa: Recorded from two vegetation units: Southern Coastal Forest (FOz 6) (Forest Biome); also a forest patch in Suurberg Quartzite Fynbos (FFq 6) (Fynbos Biome).
Assessment rationale: EOO = 130 km^2; flightless condition and severely limited range at only two locations would qualify this species for an Endangered (EN) threat category; however, it is currently assessed as Vulnerable (VU) since, (1) the EOO may be underestimated, and, (2) it is protected in Alexandria Forest, which forms part of the extended Addo Elephant National Park; nevertheless, re-assessment may be required as heavy exploitation has been reported at the forest periphery, which extends onto private land.
Conservation measures: Assessment of conservation status would be improved by a quantitative survey of forest patches and adjoining terrain in the Alexandria and Grahamstown areas; this would confirm the EOO, AOO and ecological habits; continuing protection of Alexandria Forest (Addo Elephant National Park) would be be essential for conservation of this species.



Epirinus asper

Péringuey, 1901

No synonyms

Global: LC (see IUCN Red List – DD)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'Natal (Durban, Ladysmith), Transvaal (Lydenburg)' [Durban, Ladysmith (KwaZulu-Natal), Mashishing (Mpumalanga), South Africa], lectotype: 'Durban, Natal'.

Taxonomy: Accepted species.

Distribution: Disjunct pattern on moist highlands along the edge of the E escarpment: NE Lesotho border and Mpumalanga Province, South Africa; absence of records from intervening highlands may be a collection artefact; inexact Durban type locality (black square) may lie in coastal hills, not recently recorded from Durban area.

Locality data (mean ± SD, range): Altitude: 1 763 ± 541, 1 073–3 252 m; annual rainfall: 854 ± 131, 706–1 157 mm; annual temperature (max. + min. /2): 13.7 ± 3.3, 4.6–17.5°C (N=18) (inexact Durban lectotype locality, not included).

Habitat: No quantitative assessment; DBRU collection records from finer-grained soils: sandy clay loam (1), sandy loam (4) in grassland/ pasture (5).

Food types: No quantitative assessment; DBRU collection records from cattle dung (4).

Temporal activity: Diurnal flight activity during the summer rainy season (Oct. to Mar.).

Bioregions South Africa: NE edges of Drakensberg Grassland (Gd) and Mesic Highveld Grassland (Gm) (Grassland Biome).

Assessment rationale: EOO = 40 500 km^2 (E escarpment range only); fairly widespread range in an area where natural habitat has been partly transformed (Gd: 3–16%; Gm: about 23% in occupied vegetation units); there are no quantitative data to assess possible detrimental effects of pasture improvement and development of tree plantations; currently assessed as Least Concern (LC) on basis of large range.

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, including a survey of natural grassland patches along the NE escarpment edge, coastal hills around the Durban type locality, and intervening localities; possible effects of pasture modification should also be tested; protected in uKhahlamba Drakensberg Park (World Heritage Site).

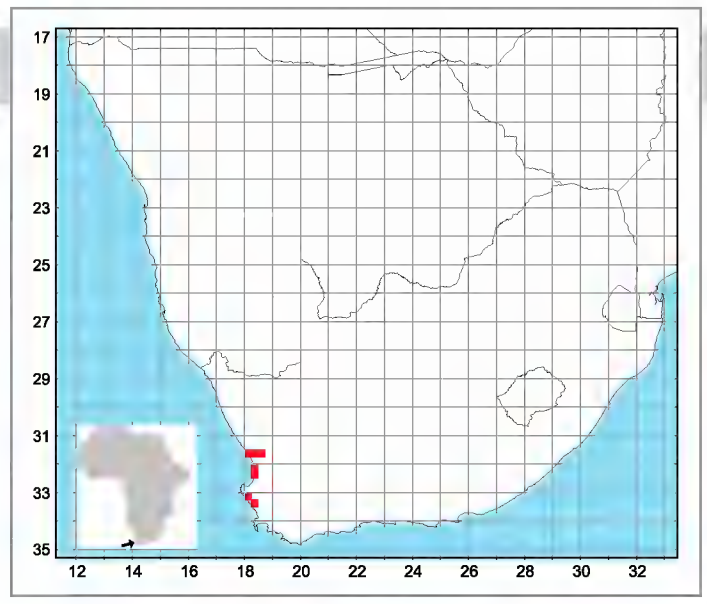
Epirinus bentoi

Ferreira, 1964a

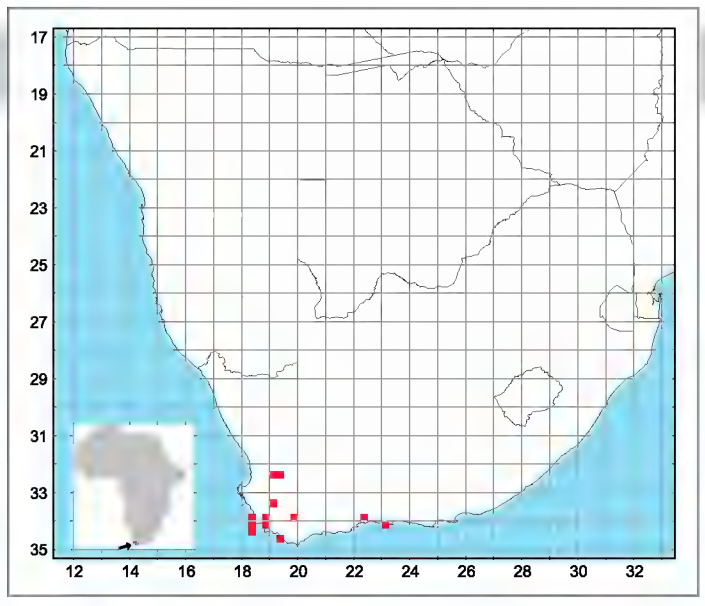
No synonyms

Global: VU
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: 'África do Sul: Província do Cabo (Eland's Bay,...)' [Elands Bay, Western Cape, South Africa].
Taxonomy: Accepted species.
Distribution: Restricted to the West Coast, Western Cape, in the winter rainfall region of South Africa.
Locality data (mean ± SD, range): Altitude: 91 ± 63, 15–199 m; annual rainfall: 226 ± 68, 157–350 mm; annual temperature (max. + min. /2): 17.3 ± 1.2, 15.7–18.9°C (N=12).
Habitat: No quantitative assessment of soil type; on Farm Geelbek: strong bias to natural shrubland (71) as opposed to sparse pasture (17) resulting from shrubland clearance; farm now restored to shrubland after incorporation into West Coast National Park; all DBRU collection records on deep coastal sands (4) in natural scrub/shrubland (4);
Food types: No quantitative assessment; DBRU collection records on cattle dung (4).
Temporal activity: Diurnal flight activity in spring to early summer (Aug. to Dec.); sclerotised adults (Aug. to Oct.), teneral adults (Oct. to Dec.).
Bioregions South Africa: Known primarily from strandveld vegetation units: Namaqualand Strandveld (SKs 7) (Succulent Karoo Biome); Lamberts Bay Strandveld (FS 1), Langebaan Dune Strandveld (FS 5) (Fynbos Biome); also Atlantis Sand Fynbos (FFd 4).
Assessment rationale: EOO = 2 700 km^2; localised within a relatively small range in an area that is subject to high transformation pressures through mining, cultivation and urbanisation (SKs 7: 10%, FS: 25-35%, FFd 4: 40%); because of small range, sensitivity to habitat transformation, and limited protection, this species is assessed as Vulnerable (VU).
Conservation measures: Assessment of conservation status would be improved by further quantitative data on ecological associations; protection of natural shrubland and continuing protection of reserves are recommended for the conservation of this species; S parts of range protected in West Coast National Park and the private Grotto Bay Nature Reserve.



Epirinus comosus

Péringuey, 1901

No synonyms

Global: DD (see IUCN Red List – DD)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'Cape Colony (Stellenbosch)' [Western Cape, South Africa], but later cited as the nearby 'Strand' on the basis of a specimen bearing a type label in Péringuey's handwriting.
Taxonomy: Accepted species.
Distribution: Mountain and coastal localities of the Western and Eastern Cape in the winter and bimodal (spring/autumn) rainfall regions, South Africa; disjunct pattern may be a collection artefact.
Locality data (mean ± SD, range): Altitude: 381 ± 536, 0–1 885 m; annual rainfall: 375 ± 85, 186–475 mm; annual temperature (max. + min. /2): 16.0 ± 2.2, 10.1–17.7°C (N=14).
Habitat: No adequate quantitative assessment; in Cape of Good Hope Nature Reserve: sampled uncommonly (6) on deep sand at a locality burnt 9–10 yr previously comprising open fynbos; absent (0) from nearby localities, one burnt 2–3 yr previously comprising a dense cover of *Restio* spp., another comprising Kikuyu pasture; one DBRU collection record from deep sand in sparse pasture.
Food types: No quantitative assessment; sampled to cattle dung.
Temporal activity: Diurnal flight activity in late winter to early summer (July to Dec.) and autumn (Apr.) coincidental with the winter, spring and autumn rainfall peaks in the winter and bimodal rainfall regions.
Bioregions South Africa: Vegetation Units in Sand Fynbos (FFd 5, FFd 10), South Strandveld (FS 7), Sandstone Fynbos (FFs 4, FFs 9, FFs 19), Granite Fynbos (FFg 3) (all Fynbos Biome); two marginal records in Shale Renosterveld (FRs).
Assessment rationale: EOO = 27 500 km^2; widespread, but AOO primarily in vegetation units characterised by sandy soils and open natural shrubland; transformation in occupied sandy vegetation units varies from 5 to 80%; may be Near Threatened (NT) in parts of its range, but currently assessed as Data Deficient (DD).
Conservation measures: A quantitative survey of the EOO, AOO and ecological associations is required to adequately assess the conservation status of *E. comosus*, particularly soil associations and effects of vegetation transformation; protected in Cape of Good Hope Nature Reserve.

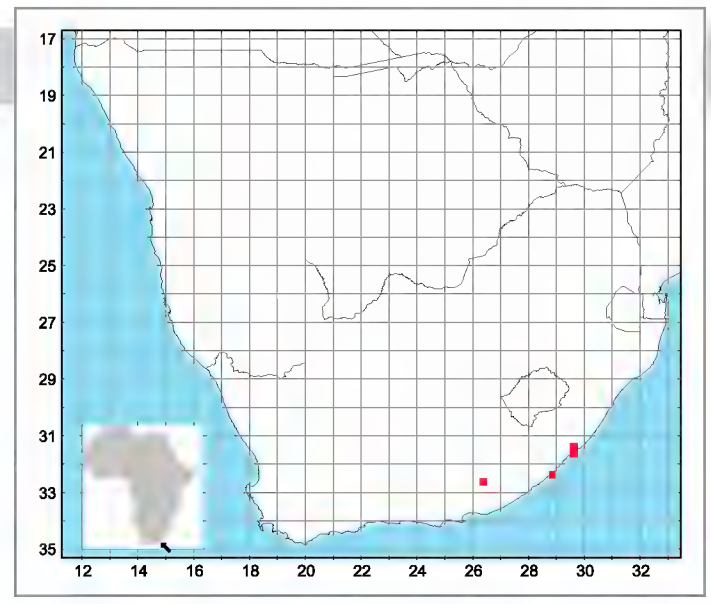
Epirinus convexus

Scholtz & Howden, 1987

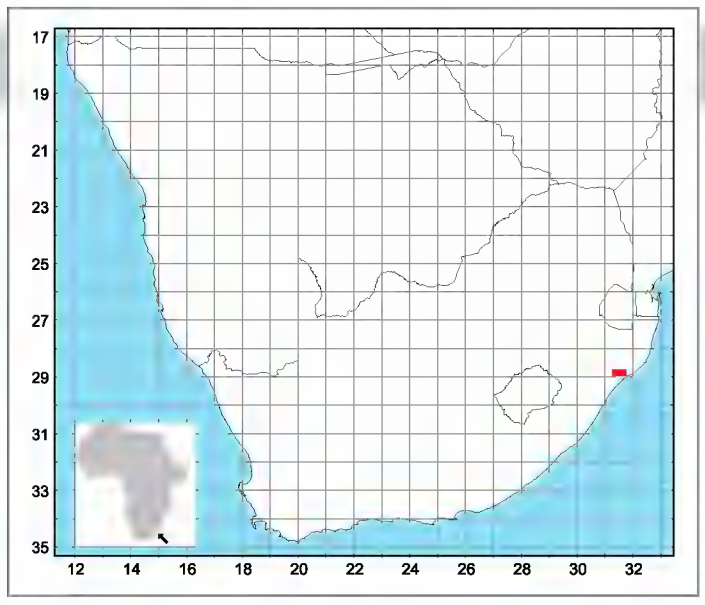
No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: 'Transkei, The Haven' [Eastern Cape, South Africa].
Taxonomy: Accepted species.
Distribution: E Eastern Cape, South Africa: coastal forest patches plus one record from forest on the S escarpment.
Locality data (mean ± SD, range): Altitude: 225 ± 319, 0–863 m; annual rainfall: 869 ± 165, 537–899 mm; annual temperature (max. + min. /2): 18.8 ± 1.2, 16.4–19.7°C (N=6).
Habitat: No quantitative assessment; all locality records from forest (8).
Food types: Unknown.
Temporal activity: Diel periodicity unknown; presumably diurnal like other *Epirinus* species; recorded sporadically in both summer rainy season (Dec., Feb.) and cool dry season (July).
Bioregions South Africa: Primarily S coastal limits of Scarp Forest (FOz 5) and S inland limits of Southern Mistbelt Forest (FOz 3).
Assessment rationale: EOO = 2 300 km^2; EOO < 5 000 km^2 with validated AOO limited to two clusters of small coastal forest patches, which, although protected, qualify this species for a threat status category, perhaps Vulnerable (VU); however, must currently be assessed as Data Deficient (DD) since precise data on range and population density are lacking; furthermore, inland forest occurrence requires validation.
Conservation measures: To assess the conservation status of this species a quantitative survey needs to be conducted in and around forest patches from E coastal Scarp Forest to Southern Mistbelt Forest; this survey should also assess ecological associations; currently protected in several coastal forest reserves, including Dwesa, Silaka, Ntsubane.



Epirinus davisi

Scholtz & Howden, 1987

No synonyms (but see Taxonomy)

Global: DD
Endemic: RSA, Eswatini

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Dhlinza Forest, Eshowe Dist.' [KwaZulu-Natal, South Africa].

Taxonomy: Accepted species, recently re-evaluated (Deschodt et al. 2019) as the senior name for the junior synonyms, *E. hluhluwensis* (also Scarp Forest) and *E. ngomae* (Southern Mistbelt Forest) (both Medina & Scholtz 2005) (see Preamble).

Distribution: Isolated patches of forest on the lower edges of the coastal escarpment, KwaZulu-Natal, South Africa; described from Dhlinza and oNgoye forests (see map above), but now includes records for junior synonyms, *E. hluhluwensis* and *E. ngomae*, plus new records from Eswatini and Nkandla Forest, towards the upper edges of the coastal escarpment (Deschodt et al. 2019).

Locality data (mean ± SD, range): Dhlinza and oNgoye forests; altitude: 258 ± 71, 208–308 m; annual rainfall: 988 ± 11, 980–995 mm; annual temperature (max. + min. /2): 20.6 ± 0.3, 20.4–20.8°C (N=2).

Habitat: All records from forest characterised by sandy loam soils; recorded from humus [forest litter].

Food types: Not known (but see data for *E. hluhluwensis* and *E. ngomae*).

Temporal activity: Flightless; diel perodicity unknown; recorded in the summer rainy season (Oct. to Dec.) in Dhlinza and oNgoye forests; data for *E. ngomae* extends seasonal extent to March.

Bioregions South Africa: Scarp Forest (FOz 5) (Forest Biome), but see data for *E. ngomae*.

Assessment rationale: EOO = 81 km^2; AOO = 30 km^2 (estimated combined area of Dhlinza and oNgoye) although addition of synonyms much increases the EOO to 11 700 km^2; known AOO would remain sufficiently limited to qualify for a threat category of Vulnerable (VU), but currently so poorly known, that it must be assessed as Data Deficient (DD); not recently recorded in either Dhlinza or oNgoye (Dec. 2014).

Conservation measures: Continuing protection of Dhlinza and oNgoye forest reserves (plus other forest patches occupied by new synonyms) is essential for the conservation of this flightless taxon; improved assessment of conservation status also requires a survey of similar regional forest patches plus their environs as well as quantitative data on the species' ecological habits.

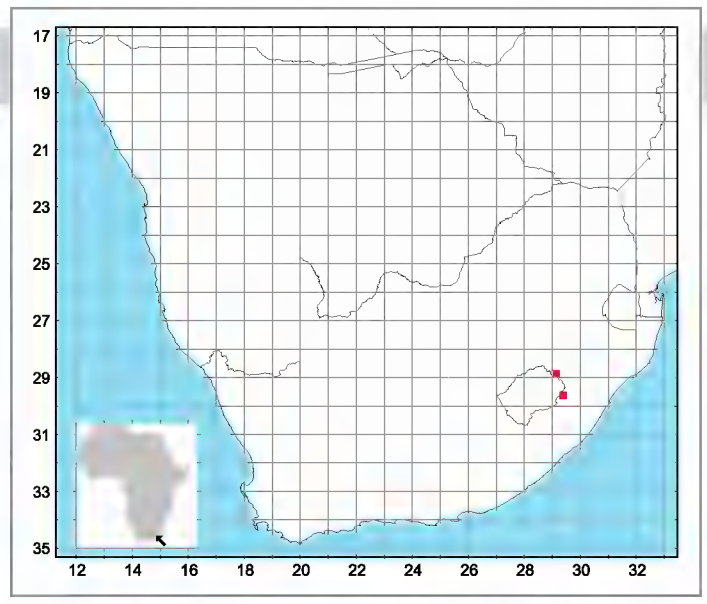
Epirinus drakomontanus

Scholtz & Howden, 1987

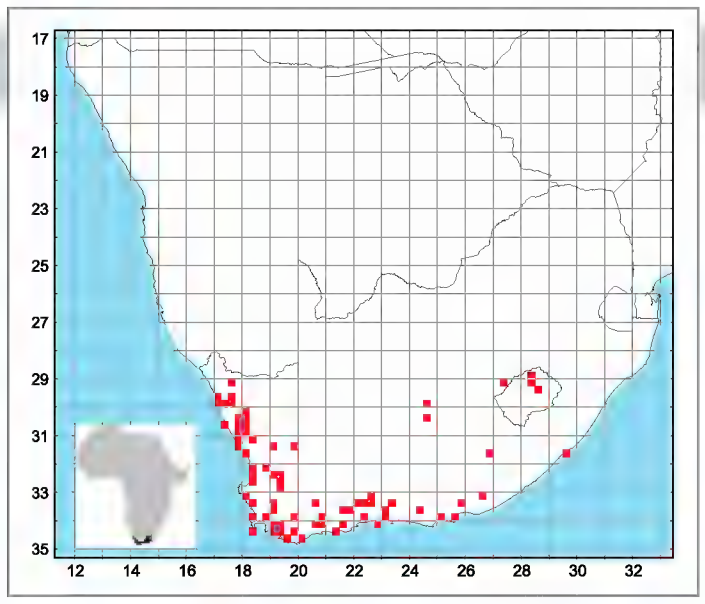
No synonyms

Global: DD
Endemic: Lesotho

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: 'Lesotho, Drakensberg (Tseke Tseke Gorge)'.
Taxonomy: Accepted species.
Distribution: Known only from extreme high altitude along the upper edge of the E escarpment just within the NE border of Lesotho.
Locality data (mean ± SD, range): Altitude: 2731 ± 473, 2 274–3 218 m; annual rainfall: 877 ± 125, 751–1 001 mm; annual temperature (max. + min. /2): 7.8 ± 2.9, 4.8–10.6°C (N=3).
Habitat: No quantitative assessment; sampled in low numbers (2) from sandy clay loam in short grassland with scattered shrubs.
Food types: No quantitative assessment; sampled to cattle dung.
Temporal activity: Diurnal flight activity in the summer rainy season (Jan. to Mar.).
Bioregions South Africa: Vegetation units: Northern Drakensberg Highland Grassland (Gd 5), Lesotho Highland Basalt Grassland (Gd 8) (Drakensberg Grassland, Grassland Biome).
Assessment rationale: EOO = 80 km^2 (probably underestimated); small known range limited to wet escarpment edge, but localities in Gd 8 suggest possible wider occurrence in the poorly protected Lesotho Highlands, which are subject to habitat transformation by cultivation and overgrazing (Gd 5, Gd 8: 7–10%); assessed as Data Deficient (DD) since it is poorly represented in collections and poorly known.
Conservation measures: A quantitative survey is required to ascertain the full EOO and ecological associations before an assessment may be made of its conservation status; the survey should determine if it is protected within the upper margins of uKhahlamba Drakensberg Park (World Heritage Site) (South Africa) or whether its range lies entirely outside of the reserve within Lesotho.



Epirinus flagellatus

(Fabricius, 1775)

= *Scarabaeus granulatus* Olivier, 1789
= *Scarabaeus scabratus* Fabricius, 1794
= *Ateuchus callosus* Thunberg, 1818
= *Epirinus vicinus* Ferreira, 1964a

Global: LC
Endemic: RSA, Lesotho, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Scarabaeus flagellatus*: 'Cap B. S.' [Cape of Good Hope, South Africa]; *S. granulatus*: Not stated; *S. scabratus*: 'Cap Bon. Spei'; *A. callosus*: Not stated; *E. vicinus*: 'África do Sul: Província do Cabo (Willowmore,...' [Willowmore, Eastern Cape, South Africa].

Taxonomy: Accepted species.

Distribution: Widespread in drier parts of the winter and bimodal rainfall regions, South Africa; scattered, high altitude occurrence to the NE in the summer rainfall region, particularly Lesotho highlands. After completion of this book at the end of 2017, this species has been recorded from Okonjima Nature Reserve, representing a first record for *Epirinus* from Namibia (Deschodt et al. 2019; see Preamble).

Locality data (mean ± SD, range): Altitude: 540 ± 557, 0–2 264 m; annual rainfall: 302 ± 164, 79–955 mm; annual temperature (max. + min. /2): 16.1 ± 1.9, 9.6–19.3°C (N=110).

Habitat: No adequate quantitative assessment; abundant in SW coastal samples: Farm Pampoenvlei shrubland on sand (159) or sandy loam (62); Modderrivier shrubland on sand (206), Groote Post pasture on sandy loam (133); DBRU collection records: clay (1), sandy clay loam (1), sandy loam (10), sand (5) in grassland/pasture (11) or Karoo scrub/shrubs (4); also fallow crop fields (2).

Food types: No quantitative assessment; DBRU collection records on cattle (18), horse (1), human (1) dung.

Temporal activity: Diurnal flight activity throughout year, but in winter rainfall region, mainly autumn to early summer seasonal activity by adults, sclerotised (mainly Mar. to Oct., peaking Mar. to May and Aug.), tenerals (Oct. to Nov.).

Bioregions South Africa: Centred on various drier bioregions of the Succulent Karoo (SK), Fynbos (F) and Albany Thicket (AT) biomes; scattered outlier highland occurrence in the Grassland Biome.

Assessment rationale: EOO = 258 000 km^2; adaptable habits indicated by widespread range across winter, bimodal and summer rainfall climates on sand and sandy loam in both shrubland and grassland cleared of natural shrubland; little transformation over the arid NW part of its range; S part of range with variable degrees of transformation; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by further quantitative data on ecological associations; protected in Namaqua and Bontebok national parks; also Cape of Good Hope Nature Reserve.

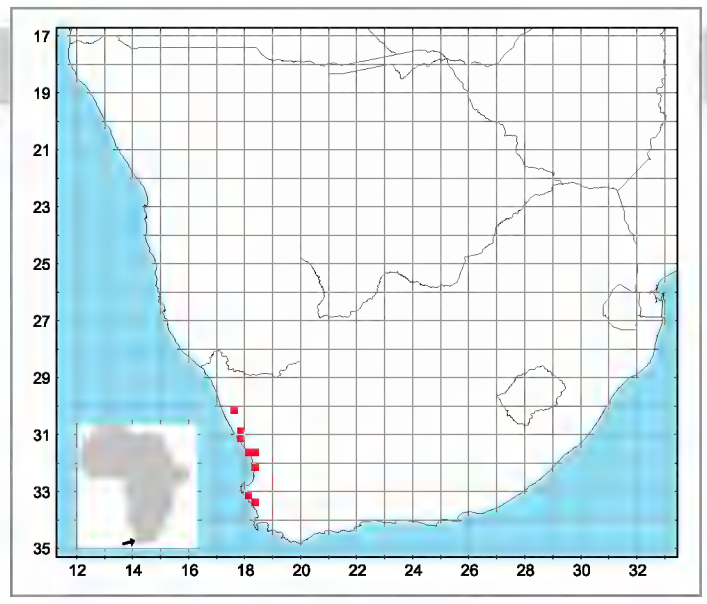
Epirinus granulatus

Scholtz & Howden, 1987

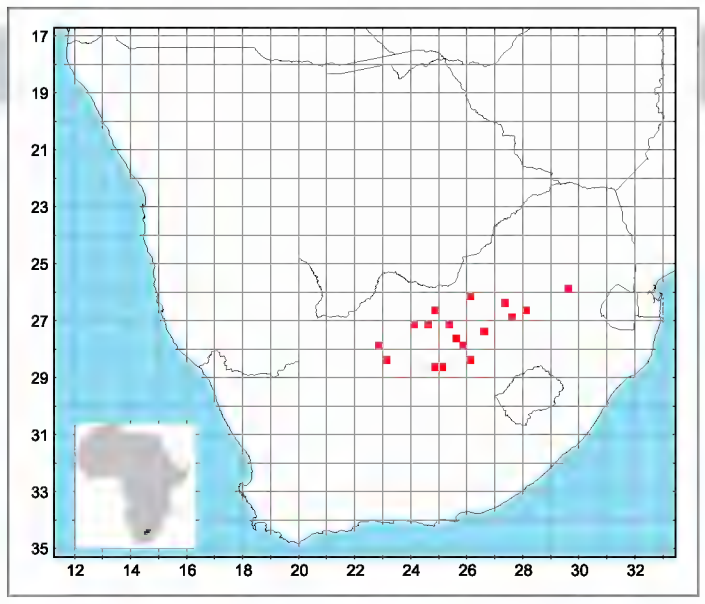
No synonyms

Global: VU
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: 'Namaqualand, Koekenaap' [South Africa].
Taxonomy: Accepted species.
Distribution: Restricted to the West Coast, Western Cape and Northern Cape, in the winter rainfall region of South Africa.
Locality data (mean ± SD, range): Altitude: 130 ± 73, 15–279 m; annual rainfall: 216 ± 90, 157–286 mm; annual temperature (max. + min. /2): 17.3 ± 1.1, 15.7–18.5°C (N=11).
Habitat: No quantitative assessment; in SW Cape: sampled from natural shrubland on inland sand dunes (37) on Farm Pampoenvlei, not recorded nearby in cleared pastures (Farm Groote Post) or nearby towards the cooler coastline (Farm Modderrivier).
Food types: No quantitative assessment; sampled to cattle dung.
Temporal activity: Diurnal flight activity during autumn and spring, sclerotised adults (mainly May to July), teneral (mainly Oct.).
Bioregions South Africa: Known from few vegetation units primarily in strandveld; Namaqualand Strandveld (SKs 7) (Succulent Karoo Biome); Lamberts Bay Strandveld (FS 1), Langebaan Dune Strandveld (FS 5) (Fynbos Biome); also Atlantis Sand Fynbos (FFd 4).
Assessment rationale: EOO = 3 400 km^2; localised within a relatively small range in an area that is subject to transformation pressures through mining, cultivation and urbanisation (SKs 7: 10%, FS: 25–35%, FFd 4: 40%); because of small range and AOO, possible sensitivity to transformation with limited protection, assessed as Vulnerable (VU).
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, particularly effects of natural shrubland clearance; protection of existing reserves probably essential for the conservation of this species; parts of S range protected in West Coast National Park.



Epirinus gratus

Péringuey, 1901

No synonyms

Global: LC (see IUCN Red List – LC)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Cape Colony (Griqualand West)' [Northern Cape, South Africa].
Taxonomy: Accepted species.
Distribution: Centred on the dry NW Highveld, South Africa.
Locality data (mean ± SD, range): Altitude: 1 379 ± 150, 1 176–1 824 m; annual rainfall: 542 ± 121, 324–733 mm; annual temperature (max. + min. /2): 17.2 ± 1.0, 14.8–19.0°C (N=23).
Habitat: No adequate quantitative assessment; in Suikerbosrand Nature Reserve: sampled on sandy clay loam in grassland (5) or open woodland (1) at 1 631–1 639 m; DBRU collection records from sand (1), sandy loam (1) in grassland (2).
Food types: No quantitative assessment; DBRU collection records from cattle dung (2).
Temporal activity: Diurnal flight activity during the summer rainy season (Nov. to May); a preponderance of Feb. collection records may indicate a late summer peak in activity.
Bioregions South Africa: Eastern Kalahari Bushveld (SVk) (Savanna Biome); N Dry Highveld Grassland (Gh) (Grassland Biome).
Assessment rationale: EOO = 74 300 km^2; widespread, but range largely coincides with vulnerable and endangered vegetation units mainly due to cultivation and invasive shrubs (mesquite in the W); extensive transformation in occupied vegetation units in both the E (Gh: 25–63%) and the W (SVk: 18–42%); however, assessed as Least Concern (LC) due to large range and protection in a number of reserves.
Conservation measures: Assessment of conservation status would be improved by further quantitative data on ecological associations, particularly possible effects of transformation of natural grasslands; protection offered in nature reserves over only a small part of its range, including Suikerbosrand, Abe Bailey, Sandveld and Nascott.

Epirinus hilaris

Péringuey, 1901

= *Endroedyantus youngae* Cambefort, 1978

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'Cape Colony (Cape Town, Stellenbosch)' [South Africa], lectotype: 'Cape Town'; *E. youngae*: 'Hawequas / 33.34S-19.08E' [all Western Cape, South Africa]

Taxonomy: Accepted species, but outlier records from higher altitude should be validated after further comparison with *E. montanus* Scholtz & Howden, 1987.

Distribution: Primarily in low-altitude localities along the S coast of South Africa with a few records from higher altitude; distribution extends across two climatic regions, winter and bimodal rainfall to edge of summer rainfall in the E; records from three disjunct centres may variously be a collecting artefact, or reflect unfavourable South Coast Renosterveld habitat (FO 8), or extensive habitat transformation.

Locality data (mean ± SD, range): Altitude: 609 ± 491, 16–1 993 m; annual rainfall: 451 ± 63, 355–546 mm; annual temperature (max. + min. /2): 15.3 ± 2.3, 9.6–18.3°C (N=17).

Habitat: No quantitative assessment; known primarily from fynbos shrubland localities with a few in forest.

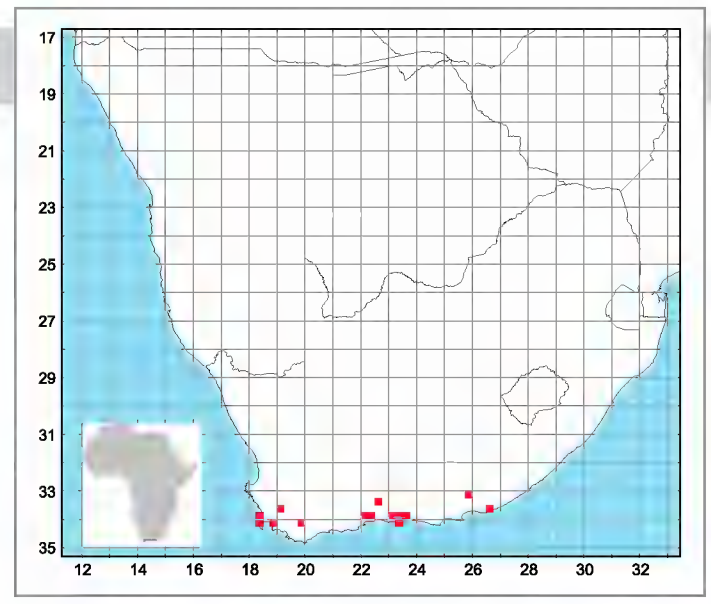
Food types: No quantitative assessment; recorded from jackal dung.

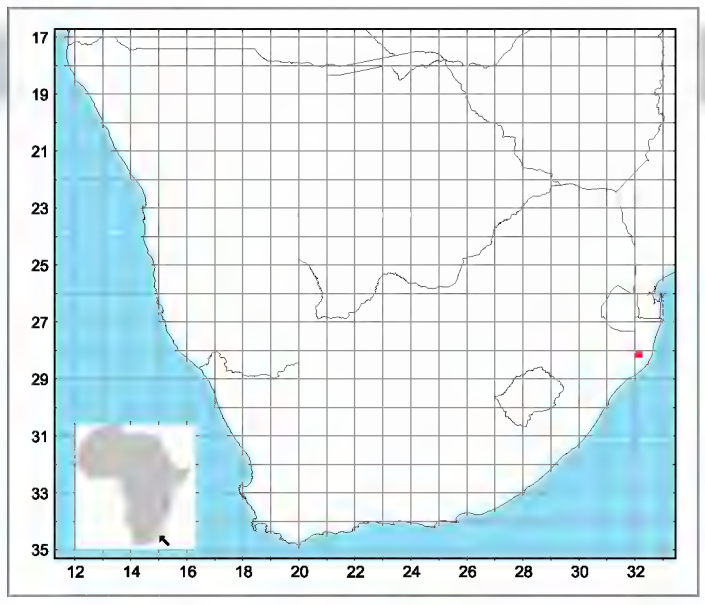
Temporal activity: Diel periodicity unknown; presumably diurnal like other *Epirinus* species; recorded during spring (Aug.) to early summer (Nov. to Jan.).

Bioregions South Africa: Centred on Sandstone Fynbos vegetation units (FFs 9, 10, 11, 13, 19) in Southwest Fynbos (FO 2) and Eastern Fynbos (FO 6) bioregions (Fynbos Biome); also Albany Thicket Biome (AT).

Assessment rationale: EOO = 29 550 km^2; ecologically poorly known; AOO may be much smaller if influenced by habitat transformation, which is sometimes extensive, sometimes limited across range (2–75%); transformation may account for disjunct records; however, assessed as Least Concern (LC) on basis of widespread EOO.

Conservation measures: Assessment of conservation status would be improved by quantitative ecological data, particularly ecological associations and possible effects of clearance of natural shrubland; a survey is also required to determine the full EOO and AOO; probably not seriously threatened, but limited known protection in a few nature reserves including Hottentots Holland.





Epirinus hluhluwensis

Medina & Scholtz, 2005 (but see Taxonomy)

No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Zululand, Hluhluwe Game Res.' [Hluhluwe–iMfolozi Game Reserve, KwaZulu-Natal, South Africa].

Taxonomy: Accepted species when the book was completed at the end of 2017, but, together with *E. ngomae* Medina & Scholtz, 2005, now a junior synonym of *E. davisi* Scholtz & Howden, 1987 (also Scarp Forest).

Distribution: Known from Hluhluwe–iMfolozi Game Reserve.

Locality data (average): Hluhluwe Game Reserve, altitude: 273 m; average rainfall: 900 mm; annual temperature (max. + min. /2): 20.5°C (N=1).

Habitat: Assumed to be forest on finer-grained soils.

Food types: Sampled to faeces bait.

Temporal activity: Not known; assumed to be flightless and diurnal like close relatives; recorded in the summer rainy season (Nov.).

Bioregions South Africa: Scarp Forest (FOz 5) (Forest Biome).

Assessment rationale: EOO = 1 580 km^2 (estimated from area occupied by an isolated scatter of FOz 5 forest patches within and close to Hluhluwe–iMfolozi Game Reserve); AOO = 50 km^2 (estimated combined area of actual forest patches); not known if it occupies all FOz 5 patches in area; although these number >10, small range might justify a Vulnerable (VU) category; however, poorly known, so currently assessed as Data Deficient (DD).

Conservation measures: Continuing protection of the scatter of Scarp Forest patches isolated in Hluhluwe–iMfolozi Game Reserve may be essential for the local conservation of this species, now synonymised with *E. davisi* by Deschodt et al. (2019); a survey of each patch in the area would be useful to accurately determine the AOO and ecological associations.

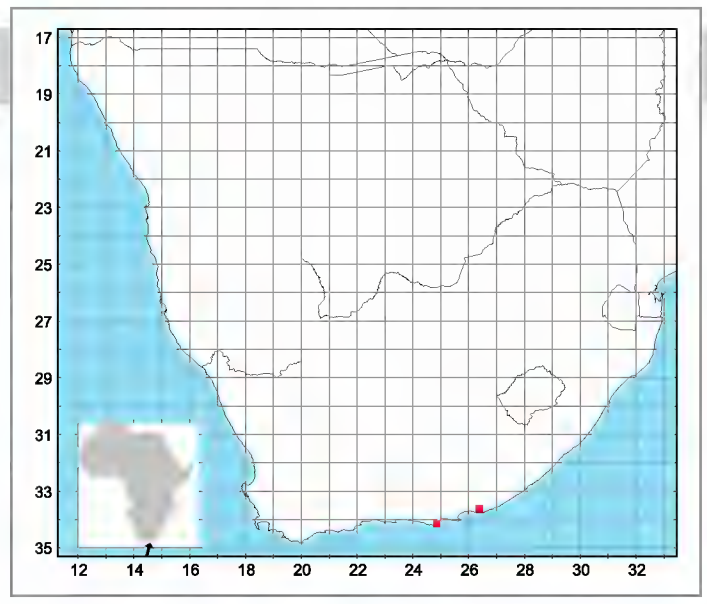
Epirinus minimus

Medina & Scholtz, 2005

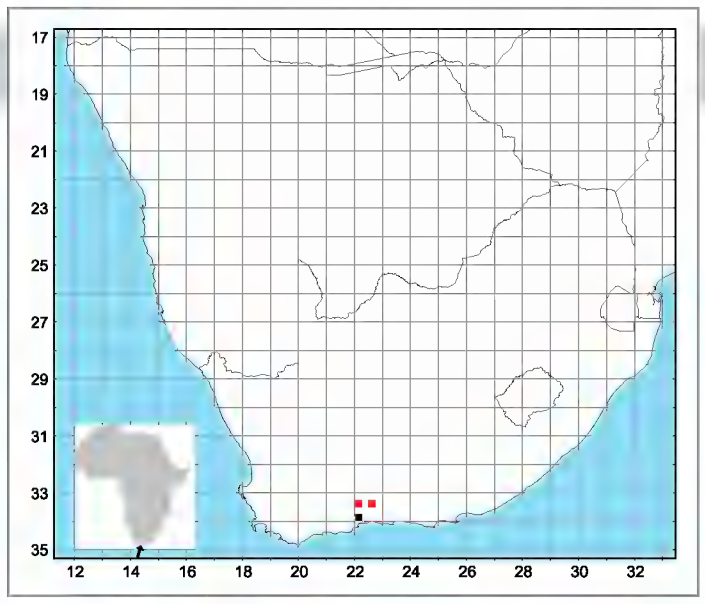
No synonyms

Global: VU
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: 'Cape Prov. Alexandria For. St.' [Eastern Cape, South Africa].
Taxonomy: Accepted species.
Distribution: SE coastal area of Eastern Cape, South Africa.
Locality data (mean ± SD, range): Altitude: 61 ± 87, 0–123 m; annual rainfall: 462 ± 29, 441–482 mm; annual temperature (max. + min. /2): 17.4 ± 0.4, 17.1–17.7°C (N=2).
Habitat: No quantitative assessment; 47 individuals in type series sifted from indigenous forest litter; three individuals from thicket at Cape St Francis appear to be the same species.
Food types: No quantitative assessment; sampled to pig dung.
Temporal activity: Flightless; diel periodicity assumed to be diurnal like other *Epirinus* spp.; recorded in mid-summer (Dec.).
Bioregions South Africa: Southern Coastal Forest (FOz 6) (Forest Biome), Algoa Dune Strandveld (AZs 1) (Azonal Coastal Vegetation).
Assessment rationale: EOO = 1 130 km^2; poorly known, but AOO may be even smaller if soil and vegetation specialisation is supported by quantitative data; would qualify for IUCN threat category status of Endangered (EN) on basis of range < 5 000 km^2 at < 5 localities, but, owing to a measure of statutory protection, currently assessed as Vulnerable (VU).
Conservation measures: As soil and vegetation associations may influence the AOO, quantitative data on ecological associations are required to improve the assessment of conservation status; to determine the full EOO, it is also necessary to conduct a survey of forest patches and dense fynbos thicket along the SE coastline, particularly on deep coastal sands; Alexandria Forest is protected in the Greater Addo Elephant National Park.



Epirinus montanus

Scholtz & Howden, 1987

No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Swartberge, Blesberg-W, 1 820 m' [mountain in Eastern Cape, South Africa].
Taxonomy: Accepted species.
Distribution: Restricted known EOO at higher altitude on low rainfall highland blocks of the Swartberg; lays to NE of coastal forest range of close relative, *E. silvestris*; one cited grid reference for Swartberg Pass (see black square) requires validation.
Locality data (mean ± SD, range): Altitude: 1 442 ± 778, 892–1 993 m; annual rainfall: 331 ± 120, 246–415 mm; annual temperature (max. + min. /2): 12.5 ± 4.1, 9.6–15.4°C (N=2) (does not include southerly record – black square).
Habitat: No quantitative assessment; two most accurate records coincide with areas of highland fynbos shrubland on sandy soils.
Food types: No quantitative assessment; unknown.
Temporal activity: Diel periodicity unknown; presumably diurnal like other *Epirinus* species; recorded during early summer (Nov., Dec.).
Bioregions South Africa: N records: North Swartberg Sandstone Fynbos (FFs 23) vegetation unit (Fynbos Biome).
Assessment rationale: EOO = 1 750 km^2 (includes non-validated southerly record); poorly known species with a very small known range across a few isolated highland blocks in the Swartberg; would qualify for IUCN threat category status of Endangered (EN) on basis of range < 5 000 km^2 at < 5 localities, but, on basis of limited information and possible under-collection, assessed as Data Deficient (DD).
Conservation measures: To adequately assess the full EOO and conservation status, a survey is required to the E and W of known localities along the higher-lying areas of the Swartberg in FFs 23, which stretches for 270 km along the mountain range; 70% of this vegetation unit is conserved; therefore, survey may result in re-assessment as Least Concern (LC).

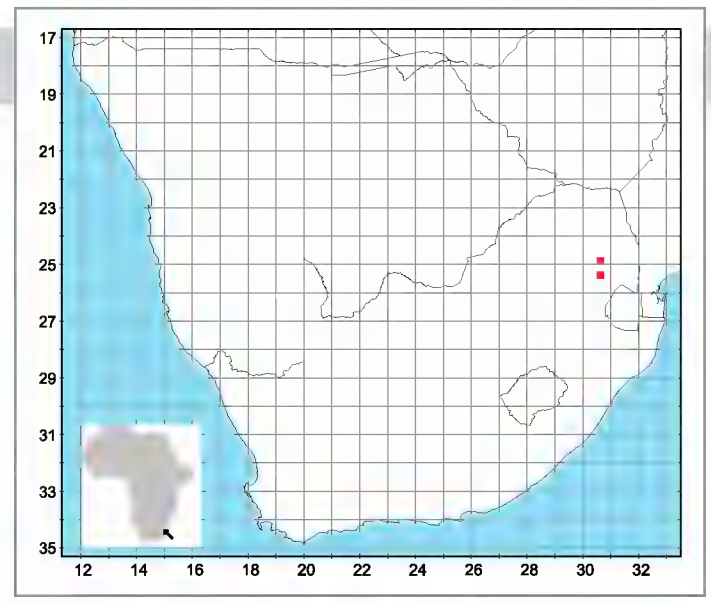
Epirinus mucrodentatus

Scholtz & Howden, 1987

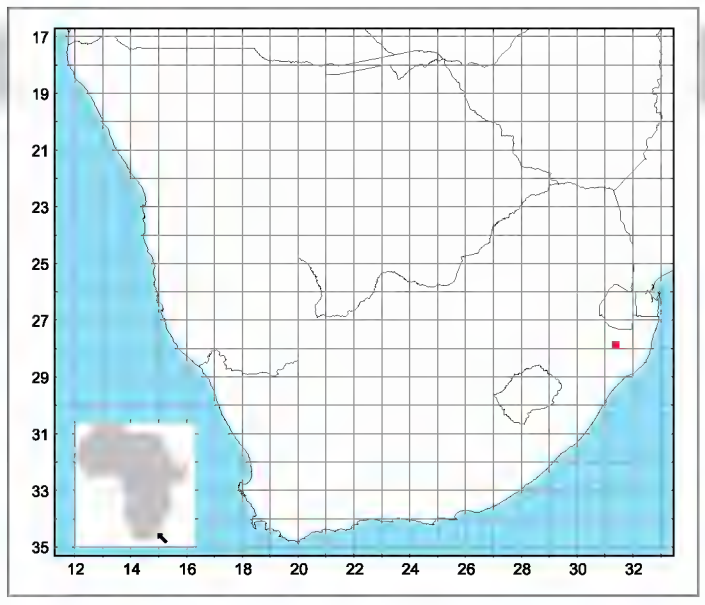
No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: 'Mount Sheba, E. Tvl' [Mpumalanga Province, South Africa].
Taxonomy: Accepted species.
Distribution: Known only from a small, moist, high altitude area close to the edge of the E escarpment in Mpumalanga, South Africa.
Locality data (mean ± SD, range): Altitude: 1 534 ± 239, 1 338–1 800 m; annual rainfall: 885 ± 78, 803–958 mm; annual temperature (max. + min. /2): 15.3 ± 1.5, 13.7–16.5°C (N=3).
Habitat: Uncertain; one Ditsong Museum record from high altitude grassland; type series known to have been recorded in a survey of mistbelt grassland and forest on Mt Sheba, but precise records not available.
Food types: A single individual sampled to carrion (Ditsong Museum); but, probably, primarily a dung-frequenting species as the type series was sampled to pig or cattle dung (precise records unavailable).
Temporal activity: Flight periodicity unknown, but assumed to be diurnal like other *Epirinus* species; recorded in the summer rainy season (Jan.).
Bioregions South Africa: Known only from the NE element of a single highland vegetation unit: Lydenburg Montane Grassland (Gm 18) (Mesic Highveld Grassland, Grassland Biome) that contains patches of Northern Mistbelt Forest (FOz 4) (Forest Biome).
Assessment rationale: EOO = 170 km^2 (presumably underestimated); size of AOO dependent on habitat association; EOO encompasses small forest patches in a grassland matrix where transformation is 23% (Gm 18), primarily due to alien vegetation; only 2.4% of the area is formally protected; would qualify for an IUCN threat category on basis of small range, but currently poorly known and assessed as Data Deficient (DD).
Conservation measures: A survey is required to determine the EOO, AOO and ecological associations before an assessment may be made of conservation status; if it is a grassland specialist, the survey should determine if the range extends to the SW element of Gm 18 and if population density is influenced by grassland modification; known to have been relatively abundant at the type locality in the private Mt Sheba Nature Reserve in 1974; current status uncertain.



Epirinus ngomae

Medina & Scholtz, 2005 (but see Taxonomy)

No synonyms

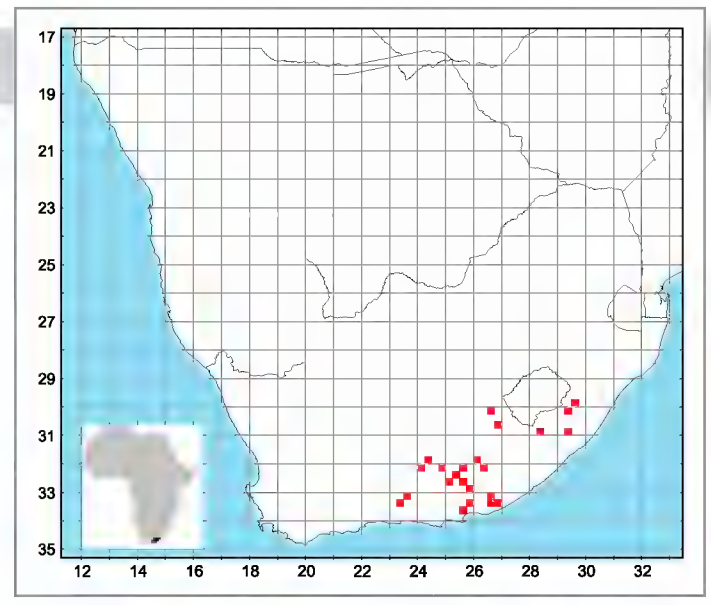
Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'KZN Ngome State Forest' [KwaZulu-Natal, South Africa].
Taxonomy: Accepted species when the book was completed at the end of 2017, but together with *E. hluhluwensis* Medina & Scholtz, 2005 now a junior synonym of *E. davisi* Scholtz & Howden, 1987.
Distribution: Known from Ngome Forest on the upper edge of the coastal escarpment, N KwaZulu-Natal, South Africa.
Locality data (mean ± SD, range): Ngome Forest, altitude: 999 m; annual rainfall: 858 mm; annual temperature (max. + min. /2): 17.6°C (N=1).
Habitat: All records from forest characterised by finer-grained sandy clay loam soils.
Food types: Poorly known; sampled using pitfalls either baited with pig dung or unbaited.
Temporal activity: Flightless; diel periodicity unknown, but presumably diurnal like other *Epirinus* species, recorded in the summer rainy season (Nov. to Mar.).
Bioregions South Africa: Southern Mistbelt Forest (FOz 3) (Forest Biome).
Assessment rationale: EOO = 765 km^2 (estimated from area occupied by an isolated scatter of forest patches at the northernmost extent of FOz 3); AOO = 40 km^2 (estimated combined area of actual forest patches with Ngome Forest by far the largest proportion, ca. 85%); not known if it occupies all FOz 3 patches in the area; as these number < 10 and represent a very small range, a Vulnerable (VU) category would be justified; however, currently assessed as Data Deficient (DD).
Conservation measures: Continuing protection of Ngome Forest Reserve would be essential for the local conservation of this flightless taxon now synonymised with *E. davisi* by Deschodt et al. (2019); to assess conservation status, a study of ecological habits is required as well as a survey of similar regional forest patches to determine population density in its AOO.

Epirinus obtusus

Boheman, 1857

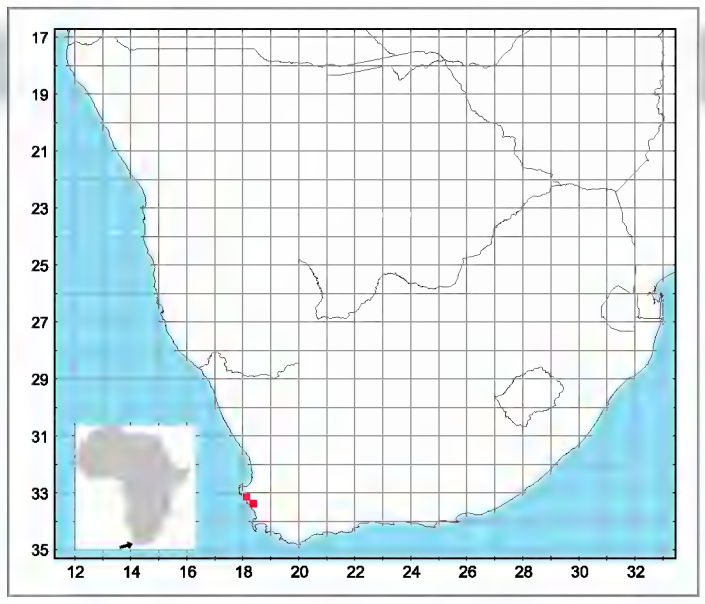


No synonyms

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: Misspelt as *Epirhinus obtusus*: 'Portum Elisabeth' [Port Elizabeth, Eastern Cape, South Africa].
Taxonomy: Accepted species.
Distribution: Somewhat disjunct pattern in dry to moist SE Highveld and mostly drier parts of transitional SE coastal regions, South Africa; disjunction may or may not be a collection artefact.
Locality data (mean ± SD, range): Altitude: 1 039 ± 513, 112–1 984 m; annual rainfall: 494 ± 147, 277–808 mm; annual temperature (max. + min. /2): 15.6 ± 1.9, 11.1–18.5°C (N=26).
Habitat: No adequate quantitative assessment; across a 500–2 800 m gradsect at 30°S: recorded only at 1 500 m (49 on sandy clay loam in natural grassland); DBRU collection records on sand (2), sandy loam (3), sandy clay loam (4) in pasture/grassland (7), scrub/shrubland (2), open woodland (1).
Food types: No quantitative assessment; DBRU collection records on dung of buffalo (3), cattle (12), zebra (1), elephant (1).
Temporal activity: Diurnal flight activity, primarily in the summer rainy season (Oct. to May).
Bioregions South Africa: In the NE: S Dry Highveld Grassland (Gh), Sub-escarpment Grassland (Gs) (Grassland Biome); in the SW: centred on Albany Thicket Biome (AT) extending into margins of Succulent Karoo (SK), Nama Karoo (NK) and Savanna (SV) Biomes.
Assessment rationale: EOO = 106 900 km^2; poorly known; may be a widespread soil and open vegetation generalist; on this assumption, assessed as Least Concern (LC), although approaching Data Deficient (DD).
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, including possible effects of habitat transformation; protected in Addo Elephant National Park.



Epirinus pseudorugosus

Medina & Scholtz, 2005

No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'West Coast N. Park' [West Coast National Park, Western Cape, South Africa].
Taxonomy: Accepted species.
Distribution: Currently known primarily from more open vegetation in a small area dominated by west coastal strandveld shrubland just to the north of Cape Town, South Africa.
Locality data (mean ± SD, range): Altitude: 63 ± 62, 15–199 m; annual rainfall: 302 ± 29, 271–350 mm; annual temperature (max. + min. /2): 15.8 ± 0.2, 15.6–16.2°C (N=7).
Habitat: No quantitative assessment of soil type; recorded on deep sands at Farm Geelbek (now West Coast National Park): few in natural shrubland (11), much more abundant where shrubland had been transformed to sparse pasture grass (170); on deep sands in shrubland at nearby Modderrivier: only 12 individuals; DBRU collection records from sand (2) in sparse pasture (2) created by clearance of natural shrubland.
Food types: No quantitative assessment; sampled to cattle dung.
Temporal activity: Diurnal flight activity during the winter rainy season (Apr. to Sept.) peaking in mid-winter (late June to early July) with limited activity in autumn (May) and spring (Aug.).
Bioregions South Africa: Known from only few vegetation units: Langebaan Dune Strandveld (FS 5), Atlantis Sand Fynbos (FFd 4), coastal patches of Hopefield Sand Fynbos (FFd 3) and Saldanha Flats Strandveld (FS 3) (all Fynbos Biome).
Assessment rationale: EOO = 230 km^2; high habitat transformation of the species range by cultivation and urbanisation (FFd 3, FFd 4: 40%; FS 3, FS 5: 35–50%), but higher abundance in pasture vegetation suggests that this species is less influenced by transformation than most endemic species; it may be less abundant than in the past at the type locality where shrubland has been permitted to regenerate across pastures after Farm Geelbek was incorporated into West Coast National Park; probably deserves at least Vulnerable (VU) status by virtue of highly restricted known range, but currently assessed as Data Deficient (DD).
Conservation measures: Further data on EOO, AOO and habitat associations are required to adequately assess the conservation status of this species; protected at type locality in West Coast National Park, but survey for relative abundance would be useful given the species bias to occurrence in pastures and the current dominance of natural shrubland within the park boundaries.

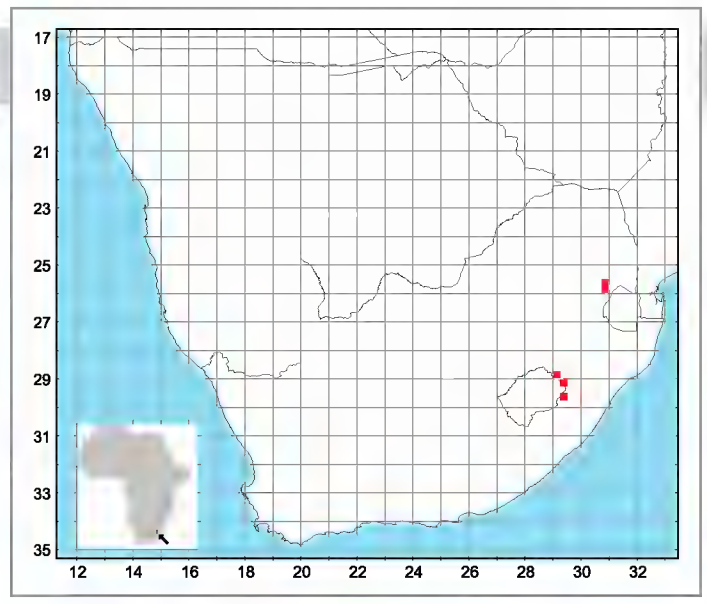
Epirinus punctatus

Scholtz & Howden, 1987

No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: 'Drakensberg, Cathedral Peak' [1 800 m, KwaZulu-Natal, South Africa].

Taxonomy: Accepted species, but specimens on Eswatini border should be validated as *E. punctatus*.

Distribution: Recorded from both high rainfall forest and grassland localities on the cool highlands of the Drakenberg Escarpment, South Africa, with the lowest locality at 1 167 m receiving high rainfall (1 157 mm p/a); unclear if disjunction is a collection artefact.

Locality data (mean ± SD, range): Average altitude: 1 820 ± 549, 1 167–2 497 m; average annual rainfall: 954 ± 242, 751–1 271 mm; average annual temperature (max. + min. /2): 13.2 ± 3.3, 9.2–17.4°C (N=5).

Habitat: No quantitative assessment; probably primarily wet highland forest patches although one available record is cited from grassland.

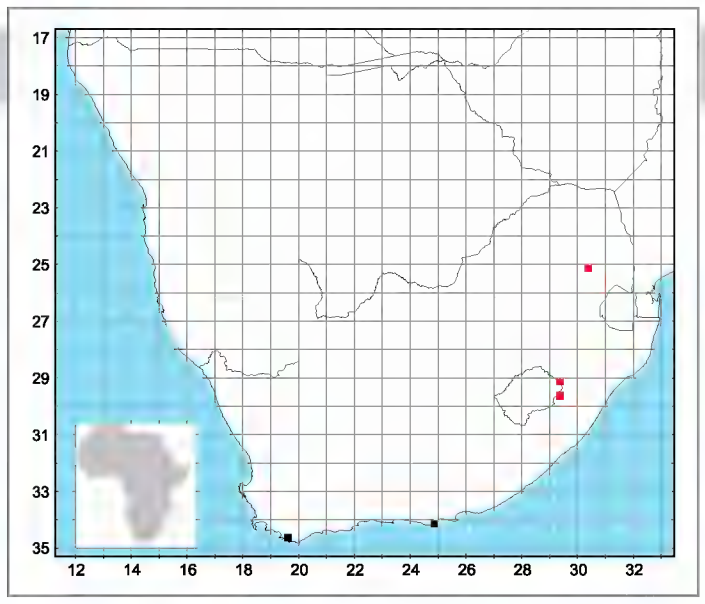
Food types: No quantitative assessment; not known.

Temporal activity: Presumably diurnal flight activity during the summer rainy season (Oct. to Mar.).

Bioregions South Africa: Although five out of eight localities are cited from forest (3) or forest stations (2), none of the cited grid references map onto forest patches although patches occur nearby; in the S: Northern Afrotemperate Forest (FOz 2); in the N: Northern Mistbelt Forest (FOz 4).

Assessment rationale: EOO = 17 500 km^2; AOO probably much smaller, centred on small patches of highland forest; known from < 10 locations across a range of < 20 000 km^2, therefore, qualifies for Vulnerable (VU) status; part of range is protected; however, poorly known ecologically, therefore, currently assessed as Data Deficient (DD).

Conservation measures: Before assessment may be made of conservation status, a quantitative survey is required along the E escarpment between the northeast border of Lesotho and northwest border of Eswatini; this should examine the EOO, AOO and ecological associations with regard to Northern Afrotemperate Forest patches, the S tip of Northern Mistbelt Forest patches, and adjacent grassland; protected in the uKhahlamba Drakensberg Park (World Heritage Site).



Epirinus pygidialus

Scholtz & Howden, 1987

No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Rep. South Africa: 75 km WSW Estcourt, Cathedral Peaks For. Stn.'.

Taxonomy: Accepted species; individuals from Western and Eastern Cape (black squares) require validation as *E. pygidialus* or a close undescribed relative.

Distribution: Drakensberg escarpment from NE Lesotho border to Mpumalanga (Mashishing); possibly also S coastline of Western and Eastern Cape, South Africa (black squares – two individuals).

Locality data (mean ± SD, range): N range: average altitude: 2 100 ± 582, 1 575–2 700 m; average annual rainfall: 815 ± 43, 782–878 mm; average annual temperature (max. + min. /2): 11.5 ± 3.5, 8.0–14.7°C (N=4). S Cape range: average altitude: 81 ± 114, 0–161 m; average annual rainfall: 435 ± 1, 434–435 mm; average annual temperature (max. + min. /2): 16.5 ± 1.0, 15.9–17.2°C (N=2).

Habitat: No quantitative assessment; NE populations recorded at 1 500 m in podocarp forest and on sandy clay loam at 2 400 m close to shrubland patches with Cape floral affinities; S Cape populations recorded on coastline, possibly close to the beach.

Food types: Unknown.

Temporal activity: Diel flight periodicity unknown; assumed to be diurnal like other *Epirinus* spp.; recorded during spring in winter rainfall region (Aug.), autumn in bimodal rainfall region (Apr.) and summer in mid-summer rainfall region (Dec., Jan.).

Bioregions South Africa: In the S Cape: Fynbos biome; in KZN: Northern Afrotemperate Forest (FOz 2); in E high altitude units: Drakensberg Grassland (Gd), Mesic Highveld Grassland (Gm) (Grassland Biome).

Assessment rationale: EOO = 18 240 km^2 or 7 810 km^2; poorly known with few, sometimes inexact, records in habitats ranging from shrub patches in grassland to fynbos or forest; assessed as Data Deficient (DD) owing to uncertain taxonomy and few widespread records.

Conservation measures: Further individuals and taxonomic study are required to determine if Eastern Cape and KwaZulu-Natal/Mpumalanga populations belong to a single species; further survey and quantitative data on ecological associations are required to determine conservation status as the few available records apparently originate from various habitat types; NE populations protected in the uKhahlamba Drakensberg Park (World Heritage Site).

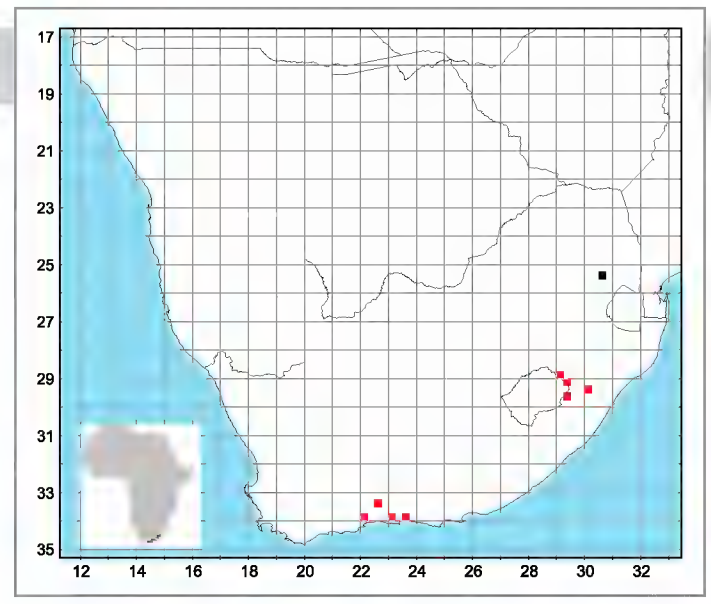
Epirinus relictus

Scholtz & Howden, 1987

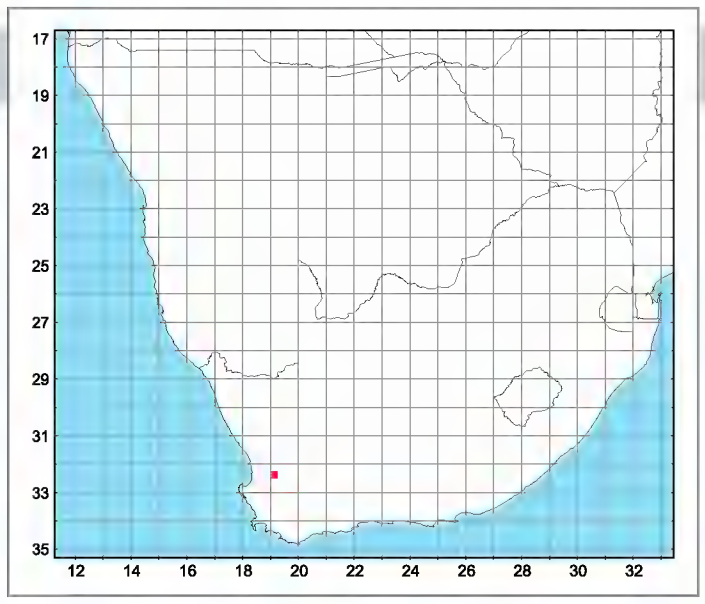
No synonyms

Global: LC (see IUCN Red List – DD)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: 'Drakensberg, Cathedral Peak' [KwaZulu-Natal, South Africa].
Taxonomy: Accepted species.
Distribution: Drakensberg escarpment along NE Lesotho border and central S coast of Eastern Cape, South Africa; unclear if disjunct pattern is real or a collection artefact; Mpumalanga record may represent mislabeled material (black square).
Locality data (mean ± SD, range): Average altitude: 1 761 ± 968, 398–3 377 m; average annual rainfall: 701 ± 220, 354–1 037 mm; average annual temperature (max. + min. /2): 11.8 ± 4.1, 3.9–16.4°C (N=11).
Habitat: No adequate quantitative assessment; recorded in fynbos shrubland and grassland at higher altitude (> 1 850 m) and in forest at lower altitude (400–1 300 m); along a gradsect (500 m to 2 800 m on latitude 29–30°S): sampled in natural grassland on sandy clay loam at 1 900 m (2.0 per trap) and close to shrubland patches with Cape floral affinities at 2 400 m (0.3 per trap).
Food types: No quantitative assessment; sampled to cattle dung.
Temporal activity: Diel flight periodicity unknown; assumed to be diurnal like other *Epirinus* spp.; recorded during summer in both the bimodal (spring autumn) and mid-summer rainfall regions (Nov. to Mar.).
Bioregions South Africa: Vegetation units: North Swartberg Sandstone Fynbos (FFs 23) (Fynbos Biome); Southern Afrotemperate Forest (FOz 1), Southern Mistbelt Forest (FOz 3); also Drakensberg Grassland Bioregion (Gd) (Grassland Biome).
Assessment rationale: EOO = 50 250 km^2 (excludes Mpumalanga record); EOO assumes continuous rather than disjunct distribution; AOO would be very much smaller; relatively poorly known ecologically, meriting a Data Deficient (DD) rating; however, assessed, here, as Least Concern (LC) as most records are from reserves.
Conservation measures: Assessment of conservation status would be improved by a quantitative survey across the known EOO; this should determine if distribution is continuous or naturally disjunct; it should also assess food and soil associations as well as apparent change in vegetation associations with altitude; protected in Tsitsikamma National Park, uKhahlamba Drakensberg Park (World Heritage Site); conservation may be dependent on continuing protection in reserves.



Epirinus rugosus

Scholtz & Howden, 1987

No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'S. Afr., Cape, Cederberg, Jeep track, 1 550 m, 32.23 S 19.08 E' [mountain range, Western Cape, South Africa].

Taxonomy: Accepted species; but paratype from Cape Town (63 km N) is *E. pseudorugosus* Medina & Scholtz, 2005; paratype from Blesberg-W in the Swartberg, (cited as Blesberg-S) subsequently described as a new species (see Preamble: *E. inparrugosus* Deschodt & Davis, 2019).

Distribution: After removal of misidentified paratypes; known by only seven individuals recorded on the Cederberg, Western Cape, South Africa.

Locality data (mean ± SD, range): Altitude: 1 293 ± 515, 944–1 885 m; annual rainfall: 273 ± 39, 247–318 mm; annual temperature (max. + min. /2): 13.2 ± 2.7, 10.1–15.1°C (N=3).

Habitat: Not known.

Food types: Not known.

Temporal activity: Flight activity assumed to be diurnal like other *Epirinus* species; recorded during the winter rainy season (Sept.) from ground traps set for 63 days.

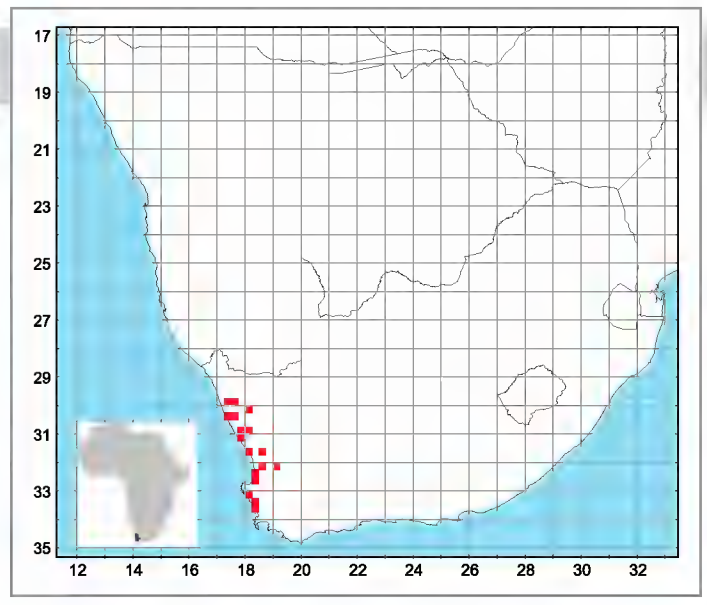
Bioregions South Africa: Vegetation unit: only Cederberg Sandstone Fynbos (FFs 4) (Fynbos Biome).

Assessment rationale: EOO = *ca.* 15 km^2; (undoubtedly underestimated as this is the area covered by three study sites within a vegetation unit that covers 2 124 km^2); even if this potential range is confirmed, with a third under protection, *E. rugosus* would qualify for an IUCN threat category; however, as EOO is uncertain and there are no recorded ecological data, it is assessed as Data Deficient (DD).

Conservation measures: A quantitative survey of EOO, AOO and ecological associations on the Cederberg is required to assess conservation status; probably protected within the 710 km^2 of the Cederberg Wilderness Area.

Epirinus scrobiculatus

Harold, 1880

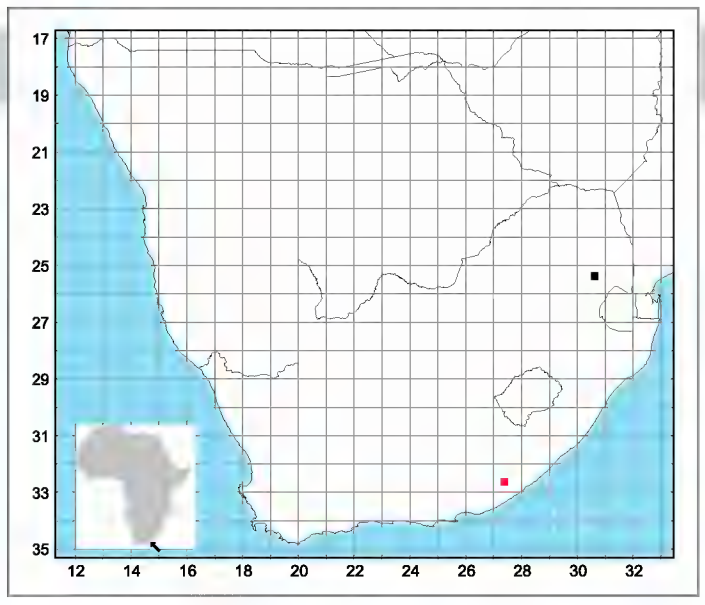


No synonyms

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Cap bon. spei (Berg!)' [Cape of Good Hope (mountain), South Africa].
Taxonomy: Accepted species.
Distribution: West Coast, South Africa; primarily in the lowland sandveld below the escarpment; mountain type locality would be atypical; citation from Namibia presumably an error.
Locality data (mean ± SD, range): Altitude: 177 ± 213, 0–899 m; annual rainfall: 197 ± 80, 98–356 mm; annual temperature (max. + min. /2): 17.3 ± 0.9, 15.7–18.9°C (N=25).
Habitat: No adequate quantitative assessment; in Western Cape: sampled primarily in shrubland on deep sand, Modderrivier (18), Pampoenvlei (30); fewer on sandy loam in shrubland, Pampoenvlei (10), or pasture, Groote Post (1); DBRU collection records on deep sand (3) in sparse grass (2) or Succulent Karoo shrubs (1).
Food types: No quantitative assessment; DBRU collection records on cattle (1) and horse (1) dung; sampled to cattle dung.
Temporal activity: Diurnal flight activity centred on the winter rainy season; in the SW Cape, active (Mar. to Nov.) peaking in autumn (May) and spring (Aug.).
Bioregions South Africa: Vegetation units in Namaqualand Sandveld (SKs), Western Strandveld (FS), Sand Fynbos (FFd) (Fynbos Biome); marginal records in Namaqualand Hardeveld (SKn) (Succulent Karoo Biome).
Assessment rationale: EOO = 15 275 km^2; widespread within a restricted range, apparently primarily on deep sand in shrubland; transformation limited in N of range (SKs: 4–8%) but extensive in the S (FFs, FS vegetation units: 25–70%); assessed as Least Concern (LC) owing to distribution centred primarily in a little-transformed region with ready attraction to dung of domestic livestock in farm rangeland.
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; protected in West Coast and Namaqua national parks.



Epirinus sebastiani

Medina & Scholtz, 2005

No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'E. Transvaal [probably Uitsoek]' [type locality (black square) considered to be an error owing to mislabeling; several paratypes from the Amatole Mountains, Eastern Cape, South Africa (red square), are considered to represent the true range of the species].

Taxonomy: Accepted species.

Distribution: Probably restricted to the Amatole Mountains, Eastern Cape, South Africa.

Locality data (mean ± SD, range): Amatole Mountains data: Altitude: 1 242 ± 232, 1 078–1 406 m; annual rainfall: 706 ± 25, 688–723 mm; annual temperature (max. + min. /2): 14.3 ± 1.2, 13.5–15.1°C (N=2).

Habitat: No quantitative assessment; recorded from litter on the floor of indigenous forest.

Food types: No quantitative assessment; sampled to faeces bait in ground traps.

Temporal activity: Flightless; diurnal activity; recorded during the summer rainy season (Nov., Dec.).

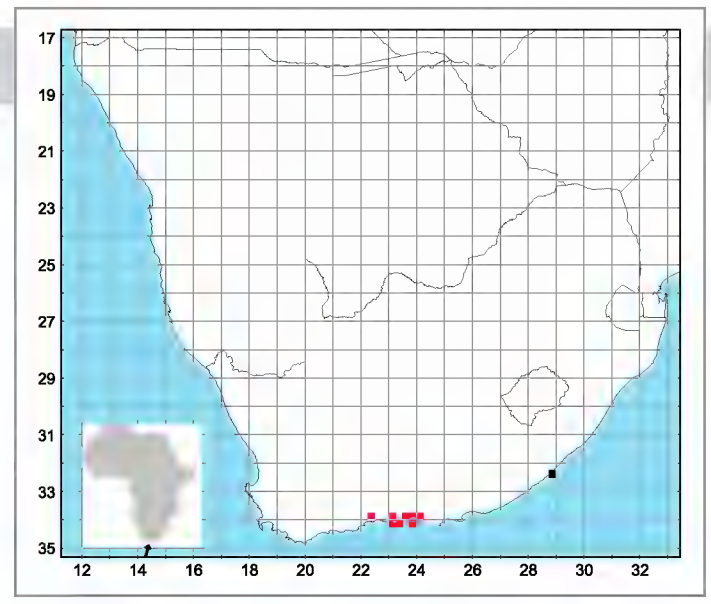
Bioregions South Africa: Southern Mistbelt Forest (FOz 3) (Forest Biome).

Assessment rationale: EOO = 130 km^2 (underestimated), AOO = 116 km^2 (area of Pirie and Isidenge forests); currently known only from two large patches of FOz 3 forest comprising the easternmost in a group centred on the Amatole Mountains; these form the SW limit of FOz 3 forest along the eastern seaboard of South Africa; species assessed as Data Deficient (DD), but may deserve at least Vulnerable (VU) status due to small EOO and restricted AOO in forest patches, at least one of which is under pressure from resource utilisation (Pirie).

Conservation measures: Protection of FOz 3 forest in the Amatole Mountains is essential for the conservation of *E. sebastiani*; a survey of these patches, and of other groups of forest patches to N and S, is required to determine its full EOO and ecological habits; a gradsect from forest fragments into grassland would confirm its limited AOO due to vegetation specialisation; protected in Isidenge State Forest.

Epirinus silvestris

(Cambefort, 1978)

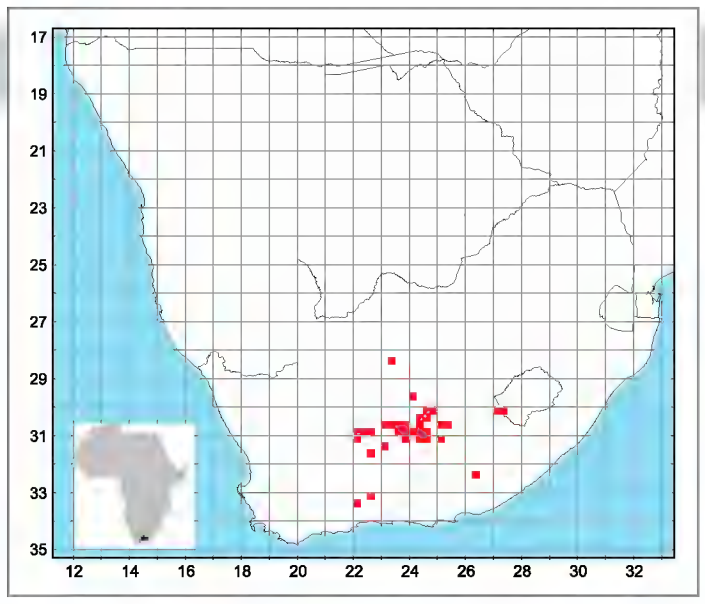


No synonyms

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Endroedyantus silvestris*: 'Harkerville Forest' [near Knysna, Eastern Cape, South Africa].
Taxonomy: Accepted species.
Distribution: Centred on a small area of forest patches along the south coast of Eastern Cape Province, South Africa; rare outlier occurrence in Dwesa Forest (black square) requires validation after further comparison with *E. convexus* Scholtz & Howden, 1987.
Locality data (mean ± SD, range): Altitude: 237 ± 244, 26–841 m; annual rainfall: 481 ± 38, 421–556 mm; annual temperature (max. + min. /2): 16.9 ± 1.1, 14.3–17.8°C (N=14) (excludes Dwesa Forest outlier (black square)).
Habitat: No quantitative assessment; many locality labels specify forest collection; soil types unknown.
Food types: No quantitative assessment; recorded on elephant dung.
Temporal activity: Flightless; diurnal activity; active in spring to early summer in the bimodal autumn/spring rainfall region (Sept. to Dec.).
Bioregions South Africa: Largely localised in S Cape patches of Southern Afrotemperate Forest (FOz 1).
Assessment rationale: EOO = 1 175 km^2 (excludes Dwesa Forest outlier); could qualify for a threat category on the basis of small EOO and even smaller AOO; specialist association with forest of which an unknown proportion has been transformed to tree plantation (at least 30 km^2 in S Cape); currently assessed as Least Concern (LC) due to distribution centred on a protected area.
Conservation measures: Conservation status is dependent on the continuing protection of low-altitude Afrotemperate forests along the coastline of the Knysna region; as these occur on both sand or finer-grained soils, an investigation is required to determine if there is any localisation in population density according to soil type; protected in the Garden Route National Park encompassing Tsitsikamma, Knysna Lakes and Wilderness.



Epirinus striatus

Scholtz & Howden, 1987

No synonyms

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Cape Karroo, Zwartskraal Farm' [N edge of Swartberg, Western Cape, South Africa].

Taxonomy: Accepted species, but status of closely related, larger-bodied populations at E edge of range needs assessment; that on the Eastern Cape highlands N of Queenstown remains unassessed; that extending across the Lesotho highlands to the Drakensberg on the NE Lesotho border has subsequently been described as a new species (see Preamble, *E. muellerae* Deschodt & Davis, 2019).

Distribution: Centred on the arid, cooler Upper Karoo with scattered records elsewhere, particularly along the N edge of the Swartberg and uplands on the SE Lesotho border.

Locality data (mean ± SD, range): Average altitude: 1 352 ± 176, 833–1 860 m; average annual rainfall: 306 ± 97, 195–696 mm; average annual temperature (max. + min. /2): 15.2 ± 1.1, 12.2–17.9°C (N=53).

Habitat: No standardised quantitative assessment; in the Northern Cape: extreme bias to cooler Upper Karoo (63.2%; 43 out of 68 study sites) compared to warmer Karoo S of Orange River (11.6%; 14 out of 121 sites); absent from deep sands of SW Kalahari and arid Bushmanland Karoo; bias to deep sand or loamy sand (5.9 per sample) compared to sandy loam (4.0/sample) or sandy clay loam (1.0/sample).

Food types: No quantitative data; attracted to composite cattle/sheep dung baits.

Temporal activity: Diurnal flight activity; seasonal occurrence reflects distribution across cool, arid areas of the bimodal (spring/autumn) and late summer rainfall regions (Sept. to June).

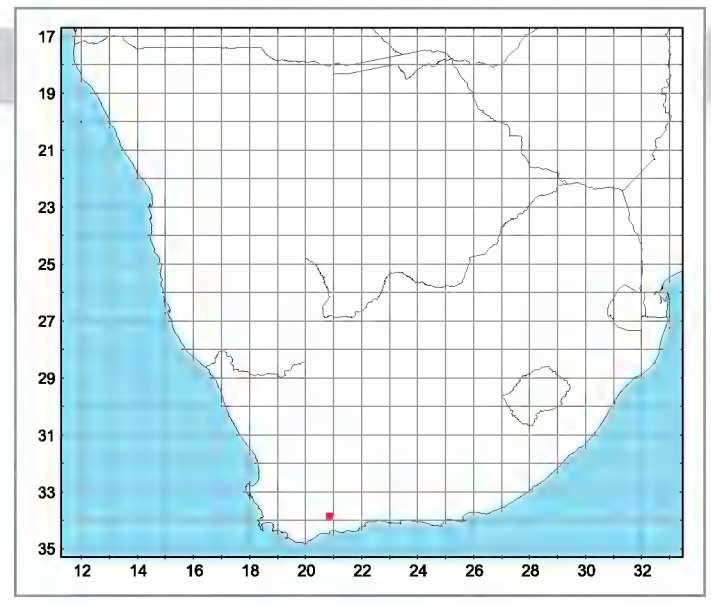
Bioregions South Africa: Primarily Upper Karoo (NKu) with scattered records in four other bioregions.

Assessment rationale: EOO = 98 000 km^2; depicted AOO may be a collection artefact emanating from high collection intensity in a quantitative study on the Upper Karoo; widespread and not under threat in natural vegetation on the farms of the Upper Karoo where habitat transformation is minimal; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by standardised quantitative data on ecological associations; not known from any protected area but well represented on farms in natural Karoo shrubland.

Epirinus sulcipennis

Boheman, 1857



No synonyms

Global: DD (see IUCN Red List – DD)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: Misspelt as *Epirhinus sulcipennis*: 'Caffraria meridionali et ad Cap. Bonae Spei.' [southern Caffraria and also Cape of Good Hope; inexact, probably = S coast of South Africa], lectotype: 'Cap B. Spei' [Cape of Good Hope].

Taxonomy: Accepted species but individuals revised by Scholtz and Howden (1987) require re-examination as they probably comprise three species; (1) *E. sulcipennis*: W localities (Grootberg confirmed); (2) closely related *E. validus* Péringuey, 1901: E localities (Eastern Cape and S Free State, but not confirmed for Scholtz and Howden citations); (3) *Epirinus* sp. nr *striatus*: N of Queenstown (confirmed).

Distribution: Probably restricted to S coastal uplands, South Africa; possibly in both winter and bimodal rainfall regions; two confirmed records at high altitude and low rainfall on Grootberg; cited occurrence in wet coastal areas at Knysna requires validation.

Locality data (average): Altitude: 1 450 m; annual rainfall: 379 mm; annual temperature (max. + min. /2): 10.9°C (N=1).

Habitat: No quantitative data; one confirmed record from an area comprising natural shrubland and sandy soils.

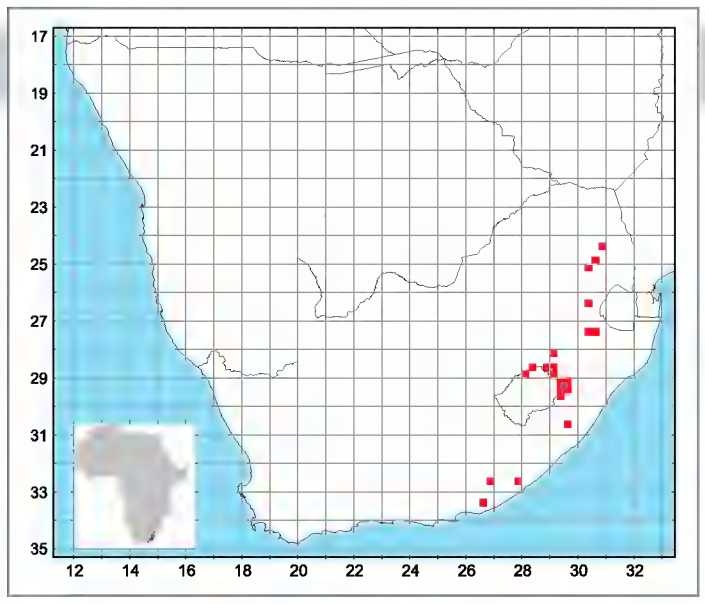
Food types: Unknown.

Temporal activity: Diel flight periodicity not known, but probably diurnal like other *Epirinus* species; recorded in Dec.

Bioregions South Africa: Confirmed occurrence only in one vegetation unit: North Langeberg Sandstone Fynbos (FFs 15) (Fynbos Biome).

Assessment rationale: EOO and AOO unknown; however, FFs 15 vegetation unit extends from Western to Eastern Cape, is only 8% transformed, and may represent a refuge (13% conserved, 45% in mountain catchment areas) where the species is not under threat; currently assessed as Data Deficient (DD).

Conservation measures: A quantitative survey of the S upland and coastal habitats in the Western and Eastern Cape is required to determine the EOO, AOO, ecological associations and conservation status as well as provide specimens for taxonomic revision; not currently known from any protected area.



Epirinus validus

Péringuey, 1901

No synonyms

Global: LC (see IUCN Red List – LC)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Transvaal (Lydenburg)' [Mashishing, Mpumalanga, South Africa].
Taxonomy: Accepted species.
Distribution: Edge of E escarpment, South Africa: at high altitude in N (Mpumalanga, KwaZulu-Natal), descending to coastal hills in S (Eastern Cape).
Locality data (mean ± SD, range): Average altitude: 1 772 ± 754, 303–3 218 m; average annual rainfall: 793 ± 119, 518–1 011 mm; average annual temperature (max. + min. /2): 13.0 ± 3.8, 4.8–21.8°C (N=26).
Habitat: No adequate quantitative assessment; at 30°S on Sani Pass: sampled in natural montane grassland on sandy clay loam: abundant at 1 900 m (42.5/trap), rare at 2 400 m (0.5) and 2 800 m (0.04), absent at lower altitude (1 500 m, 1 000 m, 500 m); DBRU collection records on sandy loam (1) in grassland (1).
Food types: No quantitative assessment; DBRU collection records on cattle dung (1); sampled in abundance to cattle dung.
Diel activity: Diurnal flight activity, primarily in the summer rainy season (Sept. to May).
Bioregions South Africa: In the N: E edge Mesic Highveld Grassland (Gm), NE edge Drakensberg Grassland (Gd); in the S: E edge Sub-Escarpment Grassland (Gs), E edge Drakensberg Grassland (Gd) (all Grassland Biome).
Assessment rationale: EOO = 52 550 km^2; widespread, but poorly known ecologically; transformation of escarpment edge vegetation units by cultivation and tree plantations would presumably be detrimental (in the N: 6–44%; in the S: 25–40%); however, assessed as Least Concern (LC) owing to abundance in protected areas along the NE border of Lesotho where transformation is only 0–7%.
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; as regards the AOO, this should include possible detrimental effects on population density of natural grassland modification to improved pastures; protected in uKhahlamba Drakensberg Park (World Heritage Site).

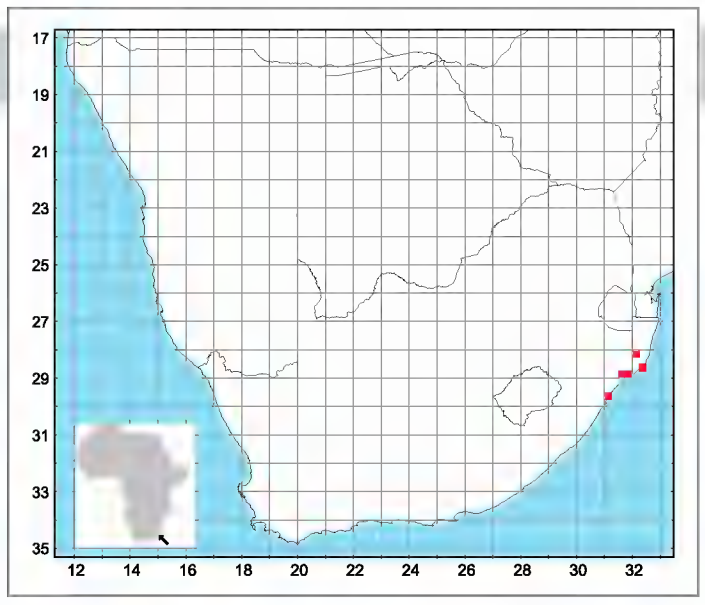
Genus *Gyronotus* van Lansberge, 1874a

Type species and designation: *Chalconotus pumilus* Boheman, 1857, by subsequent designation (van Lansberge 1874a).
Synonyms: None.
Last review: Entire genus reviewed by Scholz and Howden (1987); new species added by Davis et al. (1999b), Moretto and Perissinotto (2013); new species and a revalidation from synonomy (Deschodt & Davis 2019)

When this book was completed at the end of 2017, the long-established genus, *Gyronotus* van Lansberge, 1874a, comprised eight flightless species centred on grasslands and forests of moist coastal and upland regions along the SE seaboard of Africa from the Eastern Cape, South Africa, to NE Tanzania. However, a further three species have recently been described and one other has been revalidated from synonomy (Deschodt & Davis (2019), see Preamble). The range has been extended to SE Kenya.

Grassland spp.: Species associated with natural coastal or upland grasslands (3) have so far only been recorded in southern Africa along the SE coast (KwaZulu-Natal, South Africa) or NE escarpment (South Africa, Eswatini). Conservation status probably depends on the preservation of natural grassland.

Forest spp.: Five species associated with forest or dense shady vegetation have been recorded from the Eastern Cape in South Africa to SE Kenya. Two South African species are found in forest patches along the SE coast with the more threatened northerly species assessed as Vulnerable (VU).



Gyronotus carinatus

Felsche, 1911

No synonyms

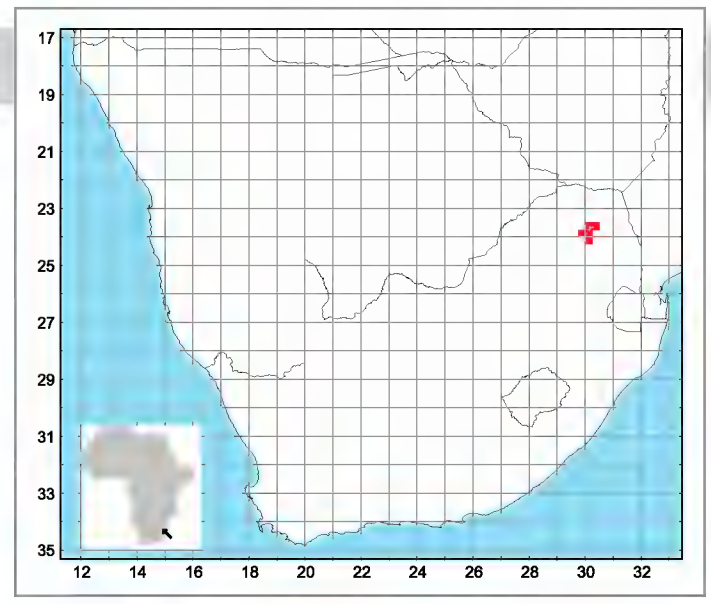
Global: VU
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'N. Calabar' [Nigeria] or 'Madagascar' [Felsche doubted that either were correct; known range of genus is SE to E Africa].
Taxonomy: Accepted species.
Distribution: Restricted to indigenous forest patches on the coastline and coastal hills of NE KwaZulu-Natal, South Africa.
Locality data (mean ± SD, range): Altitude: 115 ± 120, 2–273 m; annual rainfall: 964 ± 43, 900–998 mm; annual temperature (max. + min. /2): 21.1 ± 0.6, 20.5–21.8°C (N=5).
Habitat: No quantitative assessment of soil type; on deep dune sand near Richards Bay: only sampled in undisturbed dune forest (386), none in 0–21 yr old regenerating vegetation (grassland, dense woodland or open understorey woodland); DBRU collection records on finer-grained soils: sandy clay loam (1), sandy loam (2) in forest (4) or woodland (1).
Food types: No quantitative assessment; sampled to composite baits of cattle and pig dung.
Temporal activity: Flightless; diel periodicity not known; recorded in the summer rainy season (Oct. to Feb.).
Bioregions South Africa: Scarp Forest (FOz 5), Northern Coastal Forest (FOz 7) (Forest Biome).
Assessment rationale: EOO = 2 900 km^2; occupies a small range with an even smaller AOO due to vegetation specialisation in an area that is subject to exploitation pressures through mining of coastal dunes or forest resource utilisation; although protected in several reserves, some remain pressurised by exploitation; under these circumstances, a small AOO across a fragmented range with apparent sensitivity to disturbance, coupled with flightlessness and low vagility, suggest that the species warrants a threat category of at least Vulnerable (VU).
Conservation measures: Continuing protection of undisturbed scarp and dune forest patches would be essential for the conservation of this species; however, resource utilisation is widespread even in some officially protected forest patches; although sampled in relative abundance in Sokhulu Forest in 2000 and 2010, large parts of this forest fall within a strip mining concession; protected in Hluhluwe–iMfolozi Game Reserve, oNgoye Forest Reserve, Mapelane Nature Reserve.

Gyronotus glabrosus

Scholtz & Howden, 1987

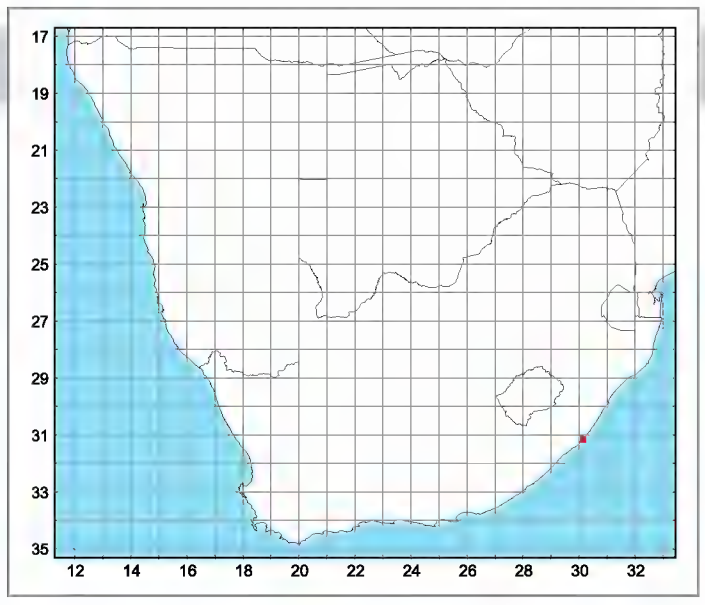


No synonyms

Global: VU
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Magoebaskloof, N. Tvl.' [Limpopo Province, South Africa].
Taxonomy: Accepted species.
Distribution: Primarily, upper NE edge of E escarpment, Limpopo Province, South Africa.
Locality data (mean ± SD, range): Altitude: 1 276 ± 585, 575–2 005 m; annual rainfall: 851 ± 76, 732–943 mm; annual temperature (max. + min. /2): 16.7 ± 3.5, 12.5–18.9°C (N=5).
Habitat: No quantitative assessment; DBRU collection data from type locality: alpine [montane] pasture on sandy loam; recent collections support occurrence in grassland habitat.
Food types: No quantitative assessment; DBRU collection data for type series: sampled to a human/cattle dung mixed bait.
Temporal activity: Flightless; diurnal activity; recorded during the summer rainy season (Dec., Feb.).
Bioregions South Africa: Vegetation units: Northern Escarpment Quartzite Sourveld (Gm 23), Woodbush Granite Grassland (Gm 25) (Mesic Highveld Grassland Bioregion, Grassland Biome); one record in Tzaneen Sour Bushveld (SVl 8) (Lowveld Bioregion, Savanna Biome).
Assessment rationale: EOO = 550 km^2; AOO would be smaller due to habitat transformation; on the basis of small range < 5 000 km^2 in only four known locations would qualify for Vulnerable (VU) status particularly as it is flightless and apparently occurs in low population density in a region subject to much transformation, primarily conversion to tree plantations (Gm 25: 69%; Gm 23: 38%).
Conservation measures: Assessment of conservation status would be improved by a survey to determine the full EOO and AOO in montane grasslands as well as the impact of habitat disturbance and transformation; protected in Lekgalameetse Nature Reserve.



Gyronotus perissinottoi

Moretto, 2013

No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'South Africa, KwaZulu-Natal, Umthamvuna Nature Reserve, Beacon Hill Section (31°00'47"S; 30°10'23"E)'.
Taxonomy: Accepted species.
Distribution: Currently known from only the type locality in Umtamvuna Nature Reserve, but possibly also represented in the past at nearby Amanzimtoti (see notes with *G. pumilus* Boheman, 1857).
Locality data (average): Altitude: 161 m; annual rainfall: 966 mm; annual temperature (max. + min. /2): 19.4°C (N=1).
Habitat: No quantitative assessment; described by Moretto and Perissinotto (2013) as 'on escarpment at the edge of riverine forest, in grassland interspersed with rocky outcrops and boulders', amongst which most individuals were recorded leading to speculation that this is where they may secrete food.
Food types: No quantitative assessment; sampled to baboon dung.
Temporal activity: Flightless; diurnal activity; recorded during the summer rainy season (Jan.).
Bioregions South Africa: Vegetation unit: Pondoland-Ugu Sandstone Coastal Sourveld (CB 4) (Indian Ocean Coastal Belt Biome).
Assessment rationale: EOO uncertain; only known from the grassland portion of a single partially forested nature reserve covering a total of 0.324 km^2; on the basis of minute range in only a single locality, would qualify for an IUCN threat category of at least Vulnerable (VU), particularly considering the degree of transformation in the coastal zone (CB 4 listed as VU; 29% transformed); however, currently assessed as Data Deficient (DD).
Conservation measures: A quantitative survey of other natural grasslands along the Pondoland and KwaZulu-Natal coastline is required to determine the EOO, AOO, ecological associations and conservation status; protected in Umtamvuna Nature Reserve (South Africa).

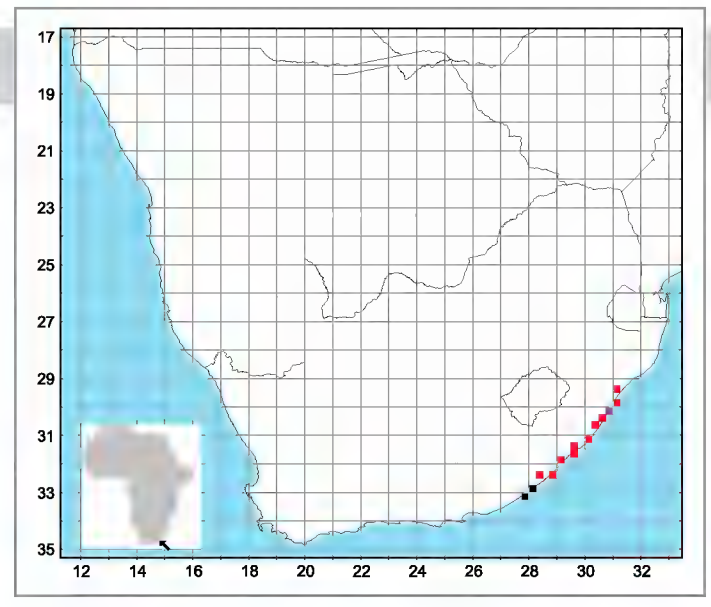
Gyronotus pumilus

(Boheman, 1857)

= *Chalconotus marginatus* Péringuey, 1888 (but see Taxonomy)

Global: LC (see IUCN Red List – LC)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: As *Chalconotus pumilus*: 'juxta fluvium Gariep' [near Orange River, South Africa; undoubtedly erroneous]. *C. marginatus*: 'East London, Cape Colony' [Eastern Cape, South Africa]

Taxonomy: Accepted species, synonymy of the larger-bodied *C. marginatus* with *G. pumilus* now overturned (revalidated by Deschodt & Davis (2019), see Preamble); in the N: larger-bodied specimens previously cited as *G. pumilus* should be compared to the recently described, *G. perissinottoi* Moretto 2013.

Distribution: Endemic to coastal forest patches of Pondoland and southern KwaZulu-Natal from East London to KwaDukuza; red squares (*G. pumilus*), purple square (?*G. perissinottoi*), black squares (*G. marginatus*).

Locality data (mean ± SD, range): Altitude: 119 ± 125, 0–418 m; annual rainfall: 914 ± 71, 741–977 mm; annual temperature (max. + min. /2): 19.5 ± 0.8, 18.4–20.9°C (N=18).

Habitat: No quantitative assessment; apparently centred on finer-grained soils in lower-lying forests; forest origin is cited on 50% of locality labels for 20 available localities; recorded as a rarity from one forest patch in Vernon Crookes Nature Reserve, but not from grassland.

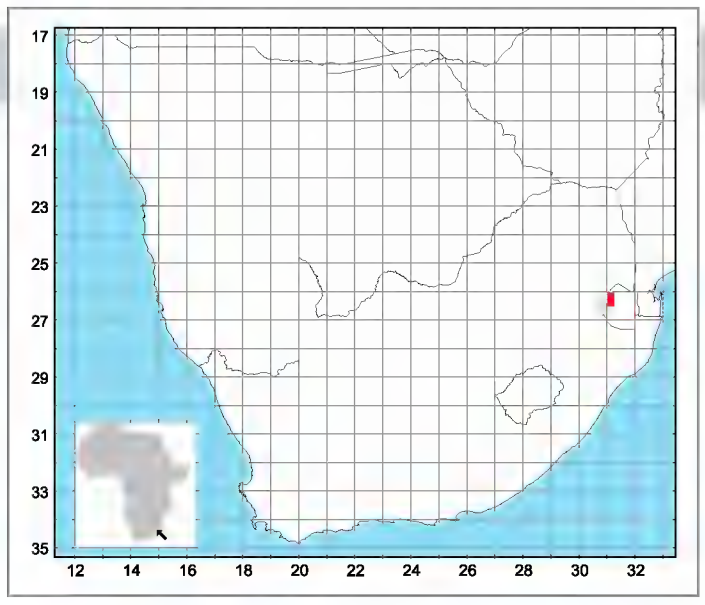
Food types: No quantitative assessment; attracted to a mixture of pig and cattle dung, but dietary preference unknown.

Temporal activity: Flightless, diurnal diel activity; recorded in the summer rainy season (Oct. to Feb.).

Bioregions South Africa: Centred on the southern half of the Scarp Forest vegetation unit (FOz 5) (Forest Biome).

Assessment rationale: EOO = 6 350 km^2; overall, 20% of FOz 5 is officially protected in reserves, but across the southern half of the unit, uncontrolled exploitation of forest, land claims and mining proposals are potential threats; in Umtamvuna Nature Reserve, *G. pumilus* occurs in forest and *G. perissinottoi* in grassland, so it is presumed that forest clearance would be detrimental to the former although only 5% of FOz 5 is currently recorded as transformed; currently assessed as Least Concern (LC) owing to moderate range size in more than 10 locations.

Conservation measures: Taxonomic examination of larger-bodied individuals is required to validate their identity as *G. pumilus* or as other species; assessment of conservation status would be improved by quantitative data on ecological associations; however, continued protection of Pondoland Scarp Forest patches along the coastline would be essential to conserve this endemic species; protection is currently offered in various nature reserves, including, Dwesa-Cwebe, Silaka, Vernon Crookes and Umtamvuna; proposals to protect this centre of endemism by the creation of Pondoland National Park remain unfulfilled at the time of writing.



Gyronotus schuelei

Moretto, 2013

No synonyms

Global: DD
Endemic: Eswatini

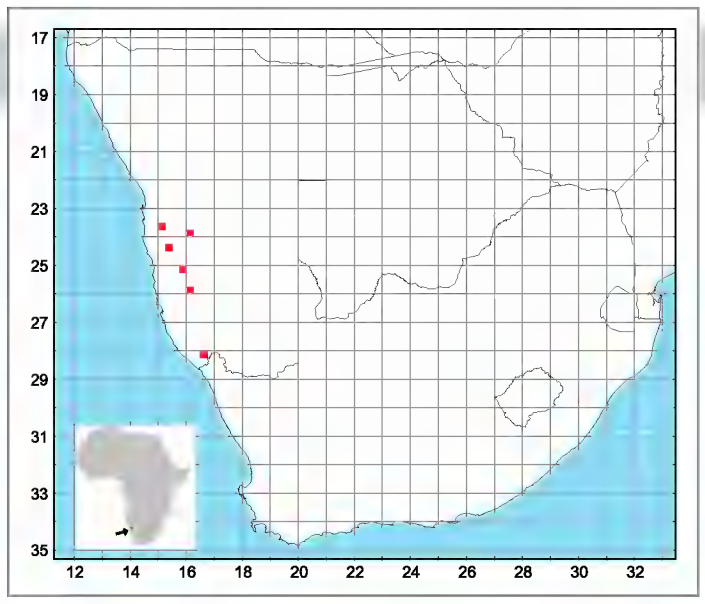
J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Swaziland, Mlilwane' [Mlilwane Wildlife Sanctuary, Eswatini].
Taxonomy: Accepted species.
Distribution: Currently known only by the holotype and allotype from W Eswatini.
Locality data (mean ± SD, range): Altitude: 870 ± 28, 850–890 m; annual rainfall: 922 ± 1, 921–923 mm; annual temperature (max. + min. /2): 19.1 ± 0.1, 19.1–19.2°C (N=2).
Habitat: No quantitative assessment; described by Moretto and Perissinotto (2013) as: 'in mountain grassland with pockets of sour bushveld'.
Food types: No quantitative assessment; holotype recorded on unidentified herbivore dung.
Temporal activity: Flightless; diurnal activity; recorded during the summer rainy season (Nov., Mar.).
Bioregions Eswatini: Straddles the boundaries of two vegetation units: KaNgwane Montane Grassland (Gm 16) (Mesic Highveld Grassland Bioregion, Grassland Biome) and Swaziland Sour Bushveld (SVl 14) (Lowveld Bioregion, Savanna Biome).
Assessment rationale: EOO = 83 km^2 (presumably underestimated); currently known only from protected areas with a combined area of 22.6 km^2; habitat transformation amounts to 21% (SVl 14) and 30% (Gm 16), but range, precise associations and degree of threat unknown; currently assessed as Data Deficient (DD).
Conservation measures: To assess conservation status; a survey is required to determine the full EOO, AOO and ecological associations in W Eswatini and (probably) across the border in South Africa; this should also determine the level of threats from tree plantations, cultivation and other disturbances; protected in Mlilwane Wildlife Sanctuary, Malalotja Nature Reserve (Eswatini).

Genus *Hammondantus* Cambefort, 1978

Type species and designation: *Hamondandantus psammophilus* Cambefort, 1978, by original designation.
Synonyms: None.
Last review: Entire genus reviewed by Scholtz and Howden (1987).

Hammondantus Cambefort, 1978 is a monotypic genus that Scholtz and Howden (1978) indicate as probably misplaced in the polyphyletic tribe, Canthonini (see placement in the phylogeny of Tarasov and Dimitrov (2016)). Most of its known range is restricted to reserves in the dune fields of the S Namib Desert.



Hammondantus psammophilus

Cambefort, 1978

No synonyms

Global: LC
Endemic: Namibia

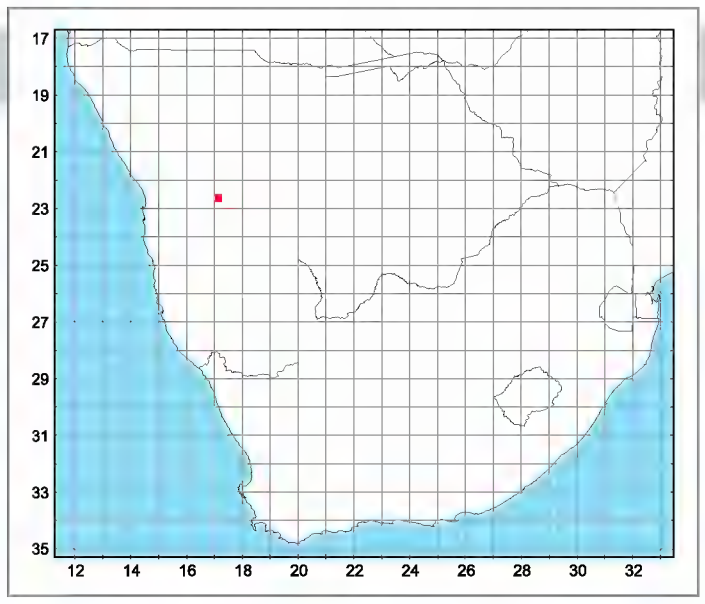
J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Sesriem Farm / Maltahöhe district' [SW Namibia].
Taxonomy: Accepted species although classification in the tribe, Canthonini, has been questioned (Scholtz & Howden 1978).
Distribution: Restricted to Namibia where it is centred on the main Namib Desert dune field; also occurs on Obib Dunes to the S.
Locality data (mean ± SD, range): Altitude: 845 ± 326, 400–1 248 m; annual rainfall: 76 ± 39, 18–131 mm; annual temperature (max. + min. /2): 16.1 ± 0.4, 15.6–16.7°C (N=6).
Habitat: Little precise data available, but recorded from sandy areas; holotype recorded from sand dunes; four of six known mapped localities also coincide with sand dunes.
Food types: Not known.
Temporal activity: Flight periodicity unknown; recorded sporadically in spring (Sept., Oct.), autumn (Mar.) and winter (June).
Ecoregions Namibia: Namib Desert (AT1315); also on Obib Dunes in the N of the Succulent Karoo (AT1322) and the W edge of the arid Namibian Savanna Woodlands (AT1316).
Assessment rationale: EOO = 13 600 km^2; although poorly known ecologically, assessed as Least Concern (LC) on basis of sizeable range and because all known localities but one lie within officially or privately protected areas.
Conservation measures: Assessment of conservation status would be improved by quantitative ecological data; protected in Namib-Naukluft and Sperrgebiet national parks and the private Namibrand Nature Reserve.

Genus *Namakwanus* Scholtz & Howden, 1987

Type species and designation: *Namakwanus irishi* Scholtz & Howden, 1987, by original designation.
Synonyms: None.
Last review: Genus created by Scholtz and Howden, 1987; revised by Deschodt and Davis (2017); new species (Deschodt & Davis 2018).

Namakwanus Scholtz & Howden, 1987 was created to accommodate a new flightless species from two different localities, one in the highlands and one from the edge of the Namib Desert in Central Namibia. The single paratype from the second locality has, subsequently, been described as a second new species (Deschodt & Davis 2017). Other species subsequently described within *Namakwanus* have been transferred by Deschodt and Davis (2017) to *Namaphilus* Deschodt & Davis, 2017, or *Versicorpus* Deschodt, Davis & Scholtz, 2011. No species accounts are provided for the two new species (Deschodt & Davis 2018) described subsequent to the completion of the book, but see Preamble.



Namakwanus irishi

Scholtz & Howden, 1987

No synonyms

Global: DD
Endemic: Namibia

| J | A | S | O | N | D | J | F | M | A | M | J |

Type locality: 'Windhoek, S.W.A.' [Namibia].
Taxonomy: Accepted species.
Distribution: Known by only four individuals from the inexact highland type locality in central Namibia.
Locality data (average): Altitude: 1 815 m; annual rainfall: 353 mm; annual temperature (max. + min. /2): 18.3°C (N=1).
Habitat: Unknown.
Food types: Unknown.
Temporal activity: Flightless; diel and seasonal periodicity unknown.
Ecoregions Namibia: Type series: NE Kalahari Xeric Savanna (AT1309).
Assessment rationale: EOO and AOO unknown; in the absence of distributional and ecological data, assessed as Data Deficient (DD).
Conservation measures: A survey of the mountains around Windhoek is required to determine the EOO, AOO and ecological associations; only then will an assessment of conservation status be possible; not currently known to occur in any protected area.

Namakwanus scholtzi

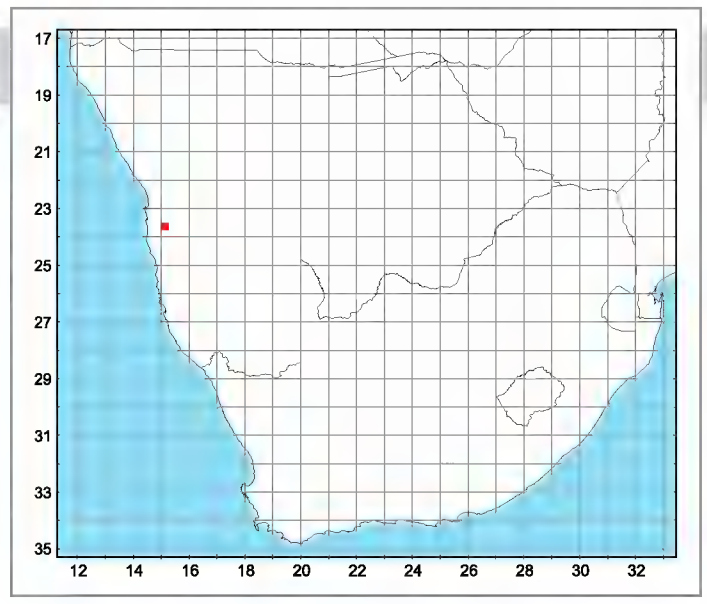
Deschodt & Davis, 2017

= *Namakwanus irishi* Scholtz & Howden, 1987 (*pars* – paratype from Kuiseb River)

Global: DD
Endemic: Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'NAMIBIA, Gobabeb, Kuiseb River, Central Namib, S. W. Afr.'.
Taxonomy: Accepted species formerly cited as a paratype of *N. irishi* Scholtz & Howden, 1987.
Distribution: Inexact locality along the Kuiseb River near Gobabeb.
Locality data (average): Altitude: 400 m; annual rainfall: 18 mm; annual temperature (max. + min. /2): 16.7°C (N=1).
Habitat: Unknown.
Food types: Unknown.
Temporal activity: Flightless; diel periodicity unknown; recorded during the late summer rainy season (May).
Ecoregions Namibia: Holotype: Namib Desert (AT1315).
Assessment rationale: EOO and AOO unknown; in the absence of distributional and ecological data, assessed as Data Deficient (DD).
Conservation measures: A survey of the area around the Kuiseb River near Gobabeb is required to determine the EOO, AOO and ecological associations; only then will an assessment of conservation status be possible; protected in the Namib-Naukluft National Park.



Genus *Namaphilus* Deschodt & Davis, 2017

Type species and designation: *Namakwanus endroedyi* Deschodt, Davis & Scholtz, 2011, by original designation.
Synonyms: None.
Last review: Genus created and reviewed by Deschodt and Davis (2017); new species (Deschodt & Davis 2018).

Namaphilus Deschodt & Davis, 2017, is a genus of flightless taxa. It was created to accommodate two species transferred from *Namakwanus* Scholtz & Howden, 1987, plus one newly described species. All species have been recorded from rocky areas in the arid Namibian savanna woodlands of central Namibia where one of the species has been observed to collect dung pellets of the rock hyrax, which defecates in middens close to each colony. No accounts are provided for the two new species (Deschodt & Davis 2018), described subsequent the the completion of the book, but see Preamble.

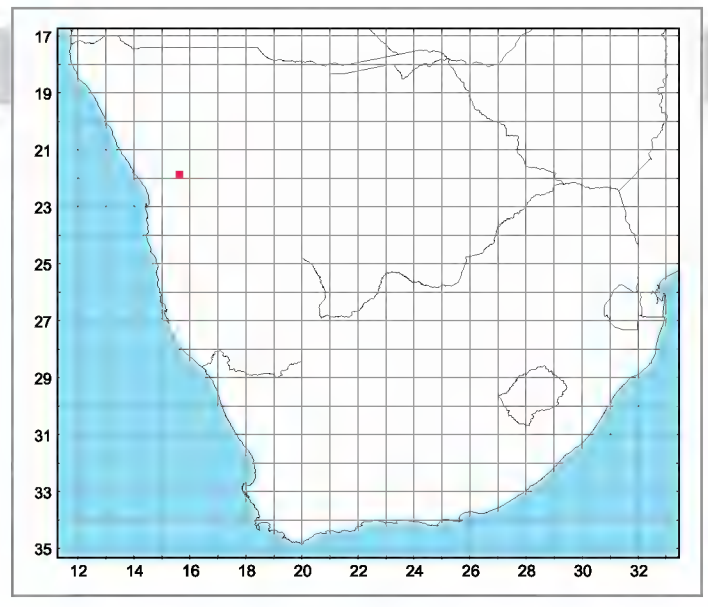
Namaphilus ameibensis

Deschodt & Davis, 2017

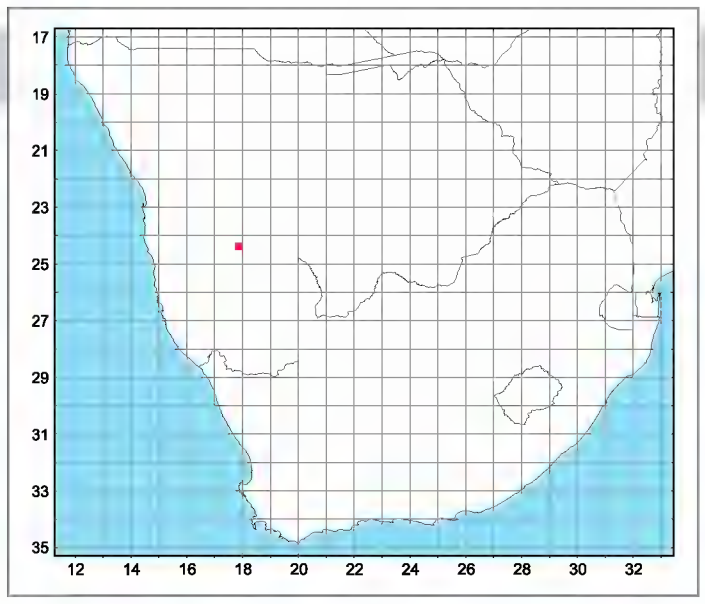
No synonyms

Global: DD
Endemic: Namibia

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: 'NAMIBIA, S.W.Afr., Erongo Mt., Farm Ameib'.
Taxonomy: Accepted species.
Distribution: Known only from the type locality in N central Namibia.
Locality data (average): Altitude: 1 197 m; annual rainfall: 210 mm; annual temperature (max. + min. /2): 17.5°C (N=1).
Habitat: No quantitative assessment; holotype collected from under a rock.
Food types: No quantitative assessment; unknown.
Temporal activity: Flightless; diel periodicity unknown; recorded during the late summer rainy season (Feb.).
Ecoregions Namibia: Namibian Savanna Woodlands (AT1316).
Assessment rationale: EOO unknown; little ecological data recorded with the single known individual (holotype female); assessed as Data Deficient (DD).
Conservation measures: A survey of the Erongo Mountains and nearby highlands is required to determine the EOO, AOO, plus ecological associations and to assess conservation status; not currently known to be protected in any reserve.



Namaphilus davisi

(Deschodt & Scholtz, 2007)

No synonyms

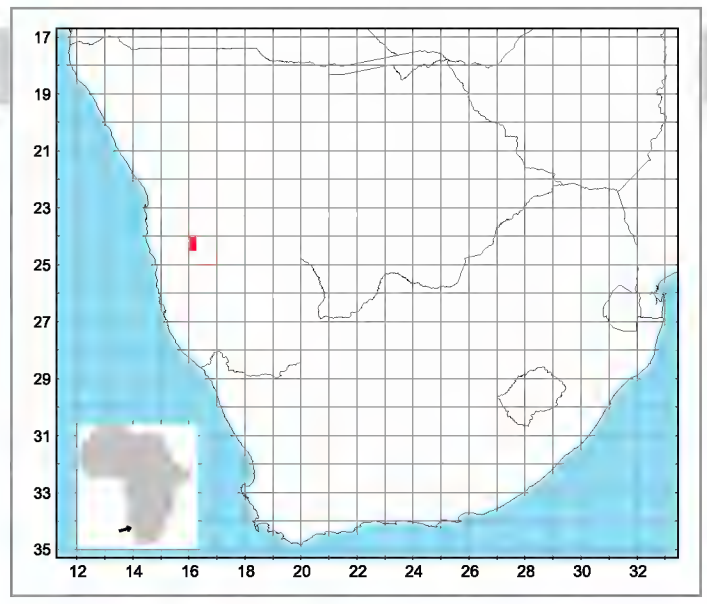
Global: DD
Endemic: Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Namakwanus davisi*: 'Hardap Dam, Namibia'.
Taxonomy: Accepted species.
Distribution: Known only by the type series found adjacent to the camp-site in the Hardap Resort, Namibia.
Locality data (average): Altitude: 1 164 m; annual rainfall: 176 mm; average temperature (max. + min. /2): 21.0°C (N=1).
Habitat: No quantitative assessment; type series collected from sandy loam soils at the base of a rocky outcrop in open scrub.
Food types: No quantitative assessment; observed to collect small pieces of dung that are broken from hyrax pellets and dragged back to their tunnels.
Temporal activity: Flightless; active during darkness, recorded during the late summer rainy season (Mar.).
Ecoregions Namibia: S Namibian Savanna Woodlands (AT1316).
Assessment rationale: EOO = 25 km^2 (probable underestimate based on the protected area around Hardap Dam); AOO probably localised to bases of rocky outcrops where rock hyrax middens provide an assured dung supply in an arid region; probably not facing any threats, but full extent of EOO currently unknown; ecological habits supported only by limited observations; therefore assessed as Data Deficient (DD).
Conservation measures: A survey to determine the full EOO is required before an assessment may be made of conservation status; localised AOO, due to association with hyrax middens, should be confirmed by gradsects away from several middens; protected in Hardap Game Park flanking the Hardap Dam.

Namaphilus endroedyi

(Deschodt, Davis & Scholtz, 2011)



No synonyms

Global: DD
Endemic: Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Namakwanus endroedyi*: 'Naukluft Mountains [Namibia]'.
Taxonomy: Accepted species.
Distribution: Known only from a few localities in the arid Naukluft Mountains, S Namibia.
Locality data (mean ± SD, range): Altitude: 1 474 ± 181, 1 266–1 589 m; annual rainfall: 155 ± 23, 128–170 mm; annual temperature (max. + min. /2): 15.7 ± 0.3, 15.5–16.1°C (N=3).
Habitat: Collected on sandy soils in shrub/woodland on a steep rocky hillside.
Food types: Sampled to banana bait, which is presumably a chance record.
Temporal activity: Flightless; one observation of diurnal foraging in cool shade between boulders on a warm day; this single live individual recorded under dry conditions during the late summer rainy season (Jan.); only dead specimens collected in Mar.
Ecoregions Namibia: Namibian Savanna Woodlands (AT1316).
Assessment rationale: EOO = 280 km^2; small known range extending across a little-transformed area; but, very poorly known ecologically; currently impossible to determine conservation status; assessed as Data Deficient (DD).
Conservation measures: Before conservation status may be assessed, a survey is required to assess the EOO, AOO and ecological associations; part of the known range protected in Namib-Naukluft National Park.

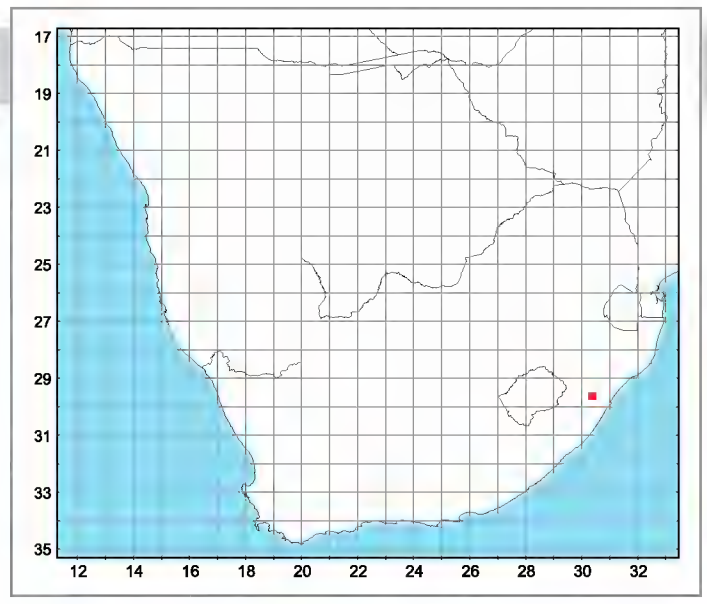
Genus *Nebulasilvius* Deschodt & Scholtz, 2008

Type species and designation: *Nebulasilvius insularis* Deschodt & Scholtz, 2008, by original designation.
Synonyms: None.
Last review: Genus created by Deschodt and Scholtz (2008).

Nebulasilvius Deschodt & Scholtz, 2008, currently comprises two small-bodied, flightless species recorded from a river bank or surface litter in different patches of Southern Mistbelt Forest, SE South Africa. Patches occur at lower altitude than that supporting *Parvuhowdenius* Deschodt & Scholtz, 2008. Given the very small known ranges and limited ecological data, both known *Nebulasilvius* species are currently assessed as Vulnerable (VU), pending surveys to provide more information.

Nebulasilvius insularis

Deschodt & Scholtz, 2008

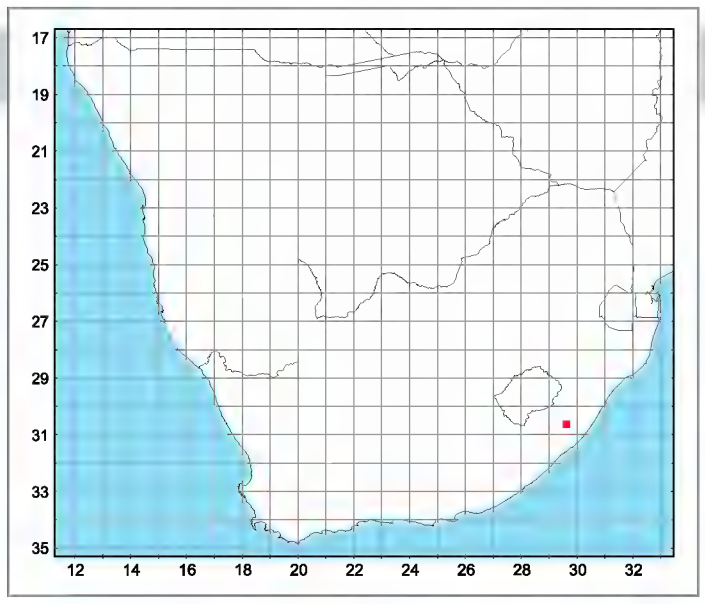


No synonyms

Global: VU
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'S.Africa; Natal Middld. Doreen Clarck Nat. R.' [Doreen Clark Nature Reserve, KwaZulu-Natal, South Africa].
Taxonomy: Accepted species.
Distribution: Known only from a single, very small forest patch on the E escarpment in the vicinity of Pietermaritzburg, KwaZulu-Natal, South Africa.
Locality data (average): Altitude: 974 m; annual rainfall: 847 mm; annual temperature (max. + min. /2): 16.9°C (N=1).
Habitat: No quantitative assessment; represented in museum collections by 104 individuals recorded on a river bank in forest.
Food types: Not known.
Temporal activity: Flightless; diel periodicity unknown; recorded in the summer rainy season (Dec.).
Bioregions South Africa: N Southern Mistbelt Forest (FOz 3) (Forest Biome).
Assessment rationale: EOO uncertain; AOO = 0.07 km^2; (approximate area of *Podocarpus* forest in Doreen Clark Nature Reserve); known only from this reserve comprising an isolated forest patch on the lower E escarpment (*Parvuhowdenius harrisoni* Deschodt & Scholtz, 2008, occurs at higher altitude along this stretch of FOz 3 forest patches); assessed as Vulnerable (VU) on the basis of extremely small known range in a single protected location; however, verging on Data Deficient (DD) considering current limited state of knowledge.
Conservation measures: A survey of other nearby patches of FOz 3 forest along the lower escarpment is required to determine if the EOO and AOO are greater than currently known; a gradsect from grassland into forest patches would confirm the vegetation specialisation and restricted AOO; protection of Doreen Clark Nature Reserve and any other occupied forest patches would be essential for the conservation of this species.



Nebulasilvius johani

Deschodt & Scholtz, 2008

No synonyms

Global: VU
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'S.Afr; S.Natal, Weza. Lower Stinkwood for.' [S KwaZulu-Natal, South Africa].
Taxonomy: Accepted species.
Distribution: Known from one or two forest patches on the E escarpment near Kokstad, KwaZulu-Natal, South Africa; validated for Weza Forest, tentative for Bangeni Forest (possibly another species).
Locality data (mean ± SD, range): Altitude: 1 179 ± 11, 1 171–1 187 m; annual rainfall: 815 ± 0.7, 814–815 mm; annual temperature (max. + min. /2): 15.4 ± 0.1, 15.3–15.4°C (N=2).
Habitat: No quantitative assessment; sifted from forest litter and recorded in ground traps.
Food types: Not known.
Temporal activity: Flightless; diel periodicity unknown; recorded in the summer rainy season (Nov.).
Bioregions South Africa: N Central patches of Southern Mistbelt Forest (FOz 3) (Forest Biome).
Assessment rationale: EOO uncertain; validated AOO = 19 km^2 (area of Weza Forest); validated type locality in Weza–Ngele has State Forest status and has become fragmented having been previously exploited for timber; on the basis of small known range in few locations deserves at least Vulnerable (VU) status although verging on Data Deficient (DD).
Conservation measures: A survey of the Eastern Mistbelt group of Southern Mistbelt Forest patches (FOz 3) is required to determine the full EOO and AOO; a gradsect from grassland into forest patches would confirm the vegetation specialisation and restricted AOO; conservation status in Weza State Forest requires further research.

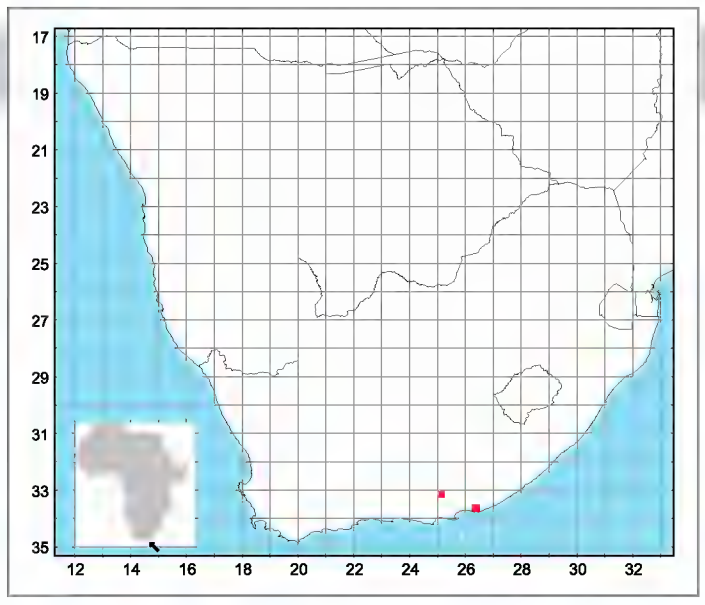
Genus *Odontoloma* Boheman, 1857

Type species and designation: *Odontoloma pauxillum* Boheman, 1857, by monotypy.
Synonyms: = *Caccobius* (*Diaglyptus*) d'Orbigny, 1902: Type species: *Caccobius metasternalis* d'Orbigny, 1902, by monotypy (subsequently, raised to generic status as *Diaglyptus* d'Orbigny, 1913, but synonymised with *Odontoloma* by Boucomont and Gillet (1927)).
Last review: Entire genus reviewed by Howden and Scholtz (1987).

The long-established genus, *Odontoloma* Boheman, 1857, currently comprises 20 Afrotropical species with distributions mostly, although not entirely, restricted to southern Africa. Most distributions occurring outside of South Africa, Namibia and Botswana are biased towards the E in Zimbabwe, Democratic Republic of the Congo (DRC) or Ethiopia, with only one species endemic to West Africa (Côte d'Ivoire). By virtue of very small body size and mostly close morphological similarity, they are difficult to separate and require revision, particularly as the alpha taxonomy is incomplete.

A total of 12 species is currently listed as being restricted to South Africa (one also in Lesotho) with three further species recorded from South Africa and Namibia (1), South Africa and Zimbabwe (1), or South Africa, Zimbabwe, Kenya and Eritrea (identified as a species complex). Species accounts are provided for these 15 taxa on the understanding that identities and distribution patterns all require validation. Brief notes are provided to point out taxonomic problems associated with each taxon.

Of the South African endemics, seven are more-or-less restricted to bimodal and/or winter rainfall regions; three to E summer rainfall and bimodal rainfall regions; two only to summer rainfall regions. However, the three other more widespread species (see previous paragraph) also occur only in summer rainfall regions in southern Africa.



Odontoloma apiculum

Howden & Scholtz, 1987

No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'S. AFRICA, C.P. Olifantskop Pass betw. Port Elizabeth and Cookhouse' [Eastern Cape, South Africa].
Taxonomy: Accepted species.
Distribution: Known only from the coastal Alexandria Forest and Olifantskop Pass along the Sundays River Valley in the bimodal spring/autumn rainfall region of the Eastern Cape, South Africa.
Locality data (mean ± SD, range): Altitude: 227 ± 148, 123–332 m; annual rainfall: 411 ± 101, 339–482 mm; annual temperature (max. + min. /2): 18.3 ± 0.9, 17.7–18.9°C (N=2).
Habitat: No quantitative assessment; recorded from an area where the natural vegetation is low succulent thicket or forest.
Food types: No quantitative assessment; no records.
Temporal activity: Humeral umbone reduced, but all related species pterous; diel periodicity unknown, but probably diurnal like other *Odontoloma* species; recorded during summer (Dec.) and autumn (May).
Bioregions South Africa: Vegetation units: Sundays Noorsveld (AT 5) (Albany Thicket Biome); Southern Coastal Forest (FOz 6) (Forest Biome).
Assessment rationale: EOO = 905 km^2 (presumably underestimated); AOO may be much more restricted than EOO if *O. apiculum* is a shade specialist; conservation status difficult to determine as range data are severely limited and ecological data are absent; known from only two localities although one is under protection; assessed as Data Deficient (DD).
Conservation measures: Before conservation status may be assessed, it is necessary to (1) determine the full EOO and AOO from a survey of the area around Alexandria Forest and Olifantkop Pass and (2) to obtain quantitative ecological data; protected in Alexandria Forest as part of the Greater Addo Elephant National Park.

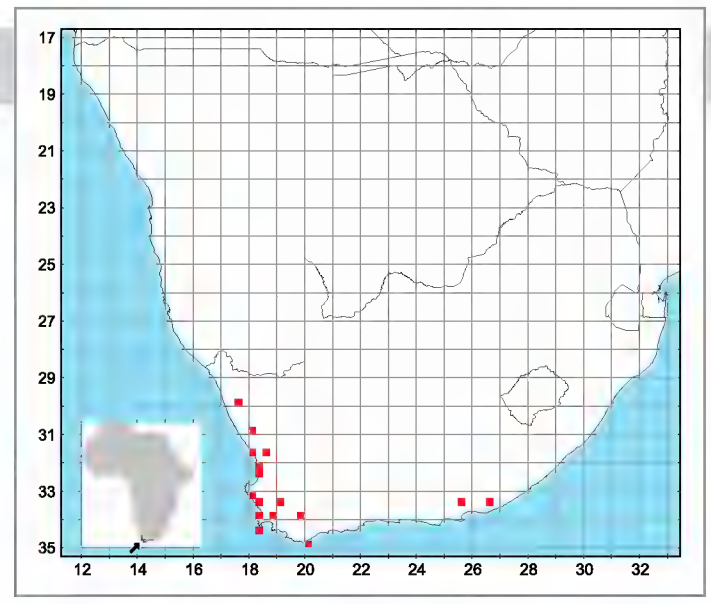
Odontoloma dentinum

(Harold, 1868a)

= *Diaglyptus serraticeps* d'Orbigny, 1913

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: As *Epirhinus dentinus*: 'Cap bon. spei' [Cape of Good Hope]; *D. serraticeps*: 'Colonie du Cap' [Cape Colony] [both SW South Africa].

Taxonomy: Accepted species.

Distribution: Primarily coastal lowlands of the winter and bimodal rainfall regions of the Western and Eastern Cape, South Africa.

Locality data (mean ± SD, range): Altitude: 179 ± 197, 0–681 m; annual rainfall: 316 ± 126, 120–595 mm; annual temperature (max. + min. /2): 17.0 ± 1.1, 14.9–18.7°C (N=21).

Habitat: In the Western Cape: well represented on deep sand to sandy loam, and natural shrubland to pasture resulting from clearance of indigenous shrubs; however, on both the cooler Cape Peninsula and drier West Coast, much more abundant in pasture (respectively, one site: 2 100; four sites: 854–1 301) than shrubland (respectively: two sites: 6–60; four sites: 2–114).

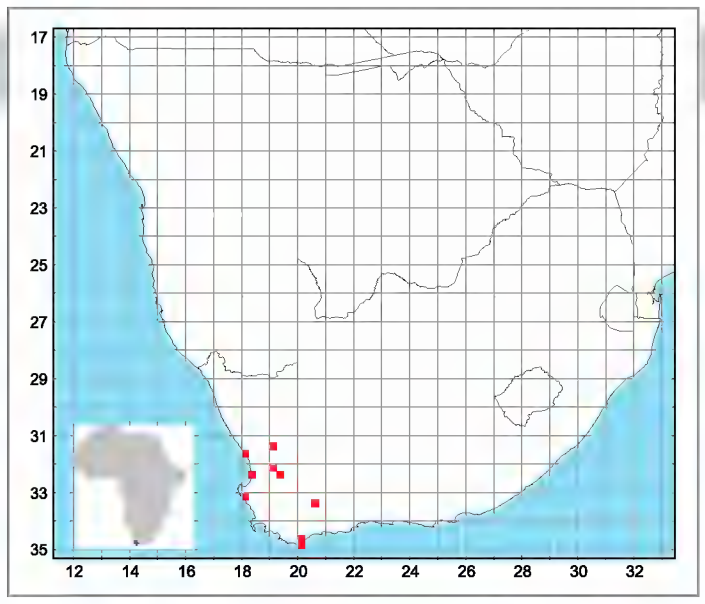
Food types: No quantitative assessment; sampled abundantly to cattle dung baits.

Temporal activity: Diurnal flight activity; recorded during most months; in Kikuyu pasture on Cape Peninsula (farm Bonne Attente), sampled from winter to spring (June to Dec.) with peak numbers from Aug. to Nov. and no activity in summer and autumn (Jan. to May).

Bioregions South Africa: Namaqualand Hardeveld (SKn), Namaqualand Sandveld (SKs) (Succulent Karoo Biome); West Strandveld (F 11), West Coast Renosterveld (FO 7) (Fynbos Biome); Albany Thicket Biome (AT).

Assessment rationale: EOO = 52 460 km^2; widespread with high frequency of records; recorded at all 11 study sites during quantitative sampling in the SW Western Cape; existing data suggest a soil generalist that is especially abundant at sites transformed from natural shrubland to pasture; therefore, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by standardised quantitative ecological data, but existing data are probably adequate; protected in West Coast National Park (Western Cape).



Odontoloma disalatum

Howden & Scholtz, 1987

No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'S. AFRICA: Cape Mt. Matjisfontein' [Western Cape, South Africa].
Taxonomy: Accepted species.
Distribution: Dry often sandy areas, primarily in fynbos vegetation of the Western Cape winter rainfall region.
Locality data (mean ± SD, range): Altitude: 289 ± 430, 0–1 415 m; annual rainfall: 266 ± 110, 157–427 mm; annual temperature (max. + min. /2): 16.9 ± 1.7, 12.5–18.5°C (N=11).
Habitat: No quantitative assessment; no records.
Food types: No quantitative assessment; holotype recorded on human dung.
Temporal activity: Apterous; diel periodicity unknown, but probably diurnal like other *Odontoloma* species; active during winter and spring (June to Oct.).
Bioregions South Africa: Centred on Northwest (FO 1) and Southwest (FO 4) Fynbos (Fynbos Biome); also Namaqualand Sandveld (SKs) (Succulent Karoo Biome).
Assessment rationale: EOO = 43 165 km^2; conservation status difficult to assess as it is ecologically poorly known; apparently restricted to dry areas in fynbos; also margins of S Succulent Karoo; occupies a wide range, but could be potentially threatened by habitat transformation as it is flightless; currently assessed as Data Deficient (DD).
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations and improved distribution data; possibly protected on the Cederberg.

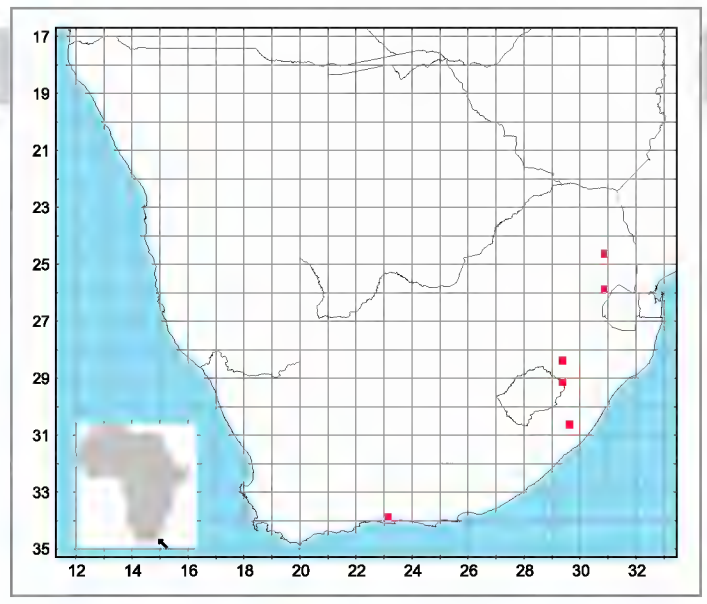
Odontoloma doubei

Howden & Scholtz, 1987

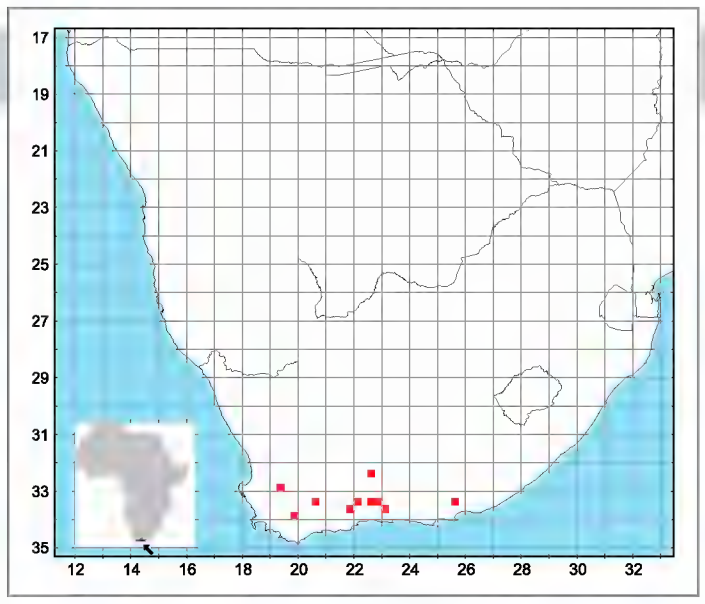
No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: 'REP. SOUTH AFRICA: Natal, 75 km WSW Estcourt, Cathedral Peaks For. Sta..... Rainbow Gorge, 1 500 m, Podocarp Forest' [Cathedral Peak Forest Station, KwaZulu-Natal, South Africa].
Taxonomy: Accepted species.
Distribution: Moist edge of E escarpment possibly mainly in shaded situations: South Africa.
Locality data (mean ± SD, range): Altitude: 1 206 ± 495, 324–1 746 m; annual rainfall: 833 ± 233, 484–1 157 mm; annual temperature (max. + min. /2): 14.8 ± 3.00, 9.2–17.4°C (N=6).
Habitat: No quantitative assessment; type locality in forest, but also recorded in coastal grassland and fynbos shrubland.
Food types: No quantitative assessment; sampled to both dung and carrion.
Temporal activity: Diel flight periodicity unknown, but probably diurnal like other *Odontoloma* species; recorded primarily during the summer rainy season (Nov. to May).
Bioregions South Africa: Primarily E edges of Grassland Biome (Mesic Highveld Grassland (Gm); Drakensberg Grassland (Gd); Sub-Escarpment Grassland (Gs)), possibly mainly in forest patches; also Eastern Fynbos-Renosterveld (FO 6).
Assessment rationale: EOO = 13 375 km^2 (gross estimate); moderately widespread, but poorly known ecologically; type locality may indicate associations primarily with shaded situations although quantitative support is required; currently assessed as Data Deficient (DD).
Conservation measures: Before conservation status may be adequately assessed a survey is required to determine the full EOO and AOO; quantitative data is required to establish ecological associations; protected in uKhahlamba Drakensberg Park (World Heritage Site).



Odontoloma endroedyi

Howden & Scholtz, 1987

No synonyms

Global: LC (see IUCN Red List – LC)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'SOUTH AFRICA: Swartberge, Hagas Farm, 1 050 m' [Eastern Cape, South Africa].
Taxonomy: Accepted species.
Distribution: Centred on dry fynbos shrubland areas in the winter and bi-modal rainfall regions of the Western and Eastern Cape, South Africa.
Locality data (mean ± SD, range): Altitude: 913 ± 539, 97–1 993 m; annual rainfall: 313 ± 70, 206–415 mm; annual temperature (max. + min. /2): 15.0 ± 2.6, 9.6–18.7°C (N=11).
Habitat: No quantitative assessment; no records.
Food types: No quantitative assessment; attracted in abundance to human dung.
Temporal activity: Diel flight periodicity unknown, but probably diurnal like other *Odontoloma* species; primarily active during spring, summer and autumn (Sept. to May).
Bioregions South Africa: Centred on Fynbos and Renosterveld (FO 1, FO 5, FO 6, FO 8) in various vegetation units: Sand Fynbos (FFd 8), Sandstone Fynbos (FFs 4, FFs 21, FFs 22, FFs 23); margins of Shale Renosterveld (FRs 6, FRs 16); marginal in Albany Thicket Biome (AT) and Lower Karoo (NKl) (Nama Karoo Biome).
Assessment rationale: EOO = 45 810 km^2; occupies a wide range with records primarily from mountain localities where natural shrubland vegetation still dominates (e.g. Matjiesfontein, Blesberg, Swartberg, Gamkaberg); on the basis of abundance in collections and the wide EOO, assessed as Least Concern (LC).
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; protected in Gamkaberg Nature Reserve, Eastern Cape, South Africa.

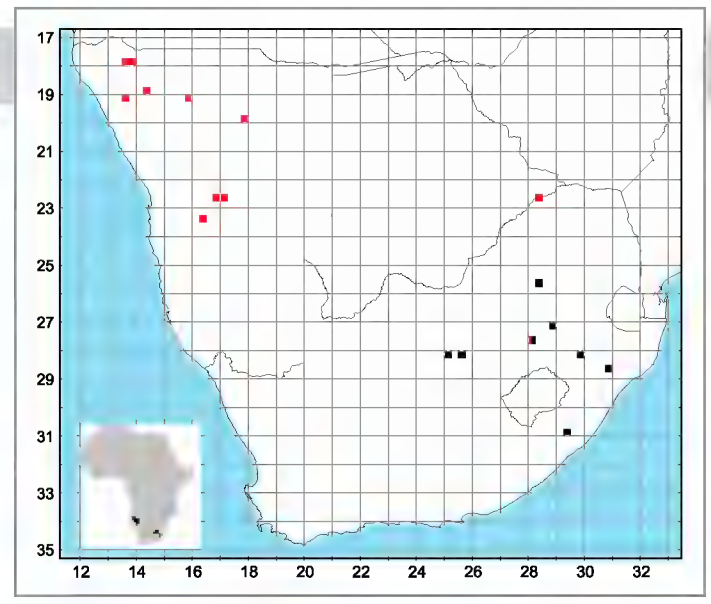
Odontoloma louwi

Howden & Scholtz, 1987

No synonyms

Global: LC (see IUCN Red List – LC)
Endemic: RSA, Namibia

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: 'NAMIBIA/S.W.A. Etosha Pan, Okaukuejo'.

Taxonomy: Accepted species, but almost all of the type series from N Namibia; most examined individuals from South Africa were excluded from the type series due to shorter parameres and doubts on their species identity.

Distribution: Disjunct pattern separated by deep Kalahari sands; type series from upland savanna of N Namibia and N South Africa (red squares); further specimens mostly recorded in grassland of the N Highveld, South Africa, but excluded from type series (black squares).

Locality data (mean ± SD, range): Type series, mainly Namibia: altitude: 1 305 ± 373, 708–1 815 m; annual rainfall: 339 ± 92, 171–512 mm; annual temperature (max. + min. /2): 18.6 ± 2.0, 16.5–22.2°C (N=11). Excluded series, South Africa: altitude: 1 345 ± 245, 846–1 678 m; annual rainfall: 675 ± 144, 433–878 mm; annual temperature (max. + min. /2): 16.5 ± 1.5, 14.4–18.9°C (N=9).

Habitat: No quantitative assessment for type series; excluded series represented in Gauteng bushveld: strong bias to finer-grained soils (sandy clay loam: 293; deep sand: 43) with generalist vegetation associations (grassland: 119; open woodland: 76; shaded thicket: 141).

Food types: No quantitative assessment.

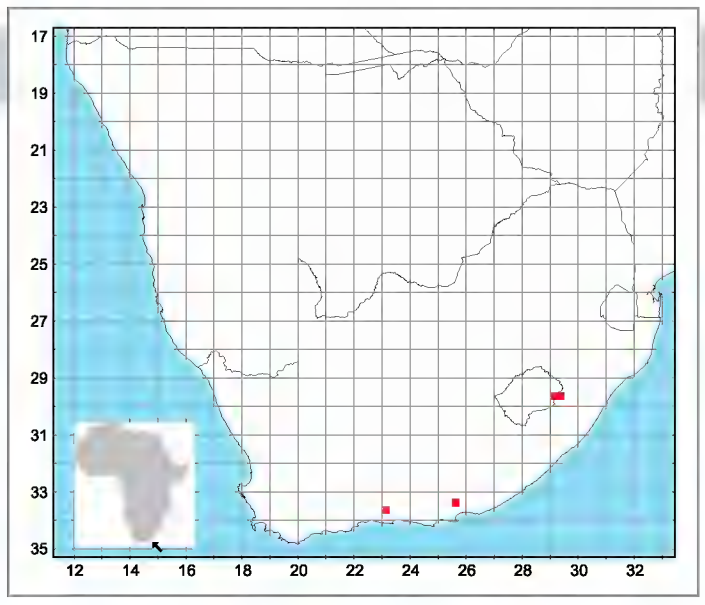
Temporal activity: Diel periodicity unknown, but probably diurnal like other *Odontoloma* species; active during the summer rainy season (Oct. to Apr.).

Ecoregions Namibia: Type series: Namibian Savanna Woodlands (AT1316), Angolan Mopane Woodlands (AT0702); NW Kalahari Xeric Savanna (AT1309).

Bioregions South Africa: Type series: Central Bushveld (SVcb) (Savanna Biome); excluded series: primarily Dry Highveld Grassland (Gh), Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs) (Grassland Biome).

Assessment rationale: EOO Namibia = 131 940 km^2; EOO South Africa = 75 220 km^2; unclear if *O. louwi* comprises one or two species; however, populations of both elements widespread, therefore, assessed as Least Concern (LC).

Conservation measures: Accurate assessment of conservation status requires further taxonomic study to establish if one or two species are included under the name, *O. louwi*; further quantitative ecological data are also required, particularly, with regard to the type series; populations represented by the type series protected in Etosha National Park; populations of excluded group not currently known from any protected area.



Odontoloma obscurum

Howden & Scholtz, 1987

No synonyms

Global: DD (see IUCN Red List – DD)
Endemic: RSA, Lesotho

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'LESOTHO, Drakensbg. Sani Pass Valley' [Lesotho: presumably upper Sani Pass].
Taxonomy: Accepted species.
Distribution: SE escarpment from high rainfall and high altitude in the N to low rainfall and low altitude in the S: Lesotho, South Africa.
Locality data (mean ± SD, range): Altitude: 1 838 ± 1 310, 97–3 218 m; annual rainfall: 688 ± 283, 389–1 001 mm; annual temperature (max. + min. /2): 11.4 ± 5.6, 4.8–18.7°C (N=5).
Habitat: On an altitudinal gradsect in KwaZulu-Natal, recorded only in low numbers at high altitude (0.3 per sample at 2 400 m, 0.8 at 2 800 m) on sandy clay loam in grassland.
Food types: No quantitative assessment; attracted to cattle dung.
Temporal activity: Diel flight periodicity unknown, but probably diurnal like other *Odontoloma* species; active primarily during the summer rainy season (Jan. to May).
Bioregions South Africa: Drakensberg Grassland (Gd) (Grassland Biome); Albany Thicket Biome (AT); Eastern Fynbos-Renosterveld Bioregion (FO 6) (Fynbos Biome).
Assessment rationale: EOO = 8 020 km^2 (gross underestimate); poorly known species both biogeographically and ecologically; therefore, assessed at Data Deficient (DD).
Conservation measures: To assess conservation status, a quantitative survey is required to determine the full EOO, AOO and ecological associations; protected in the uKhahlamba Drakensberg Park (World Heritage Site).

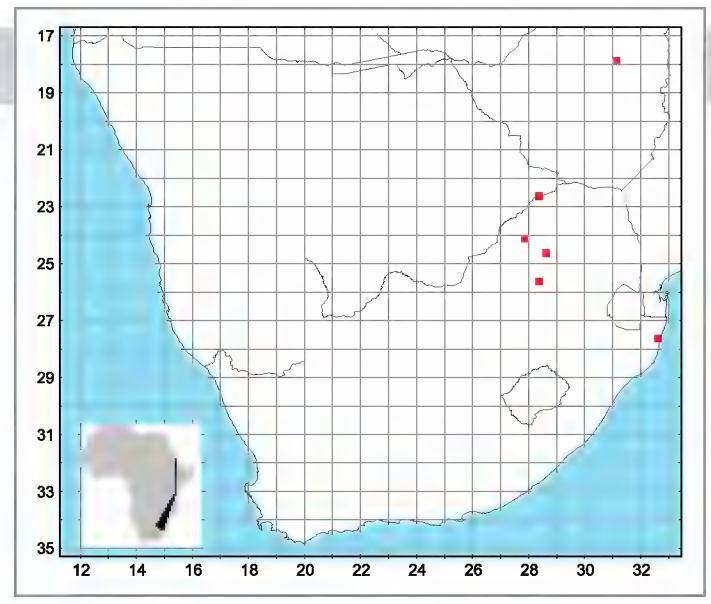
Odontoloma pauxillum

Boheman, 1857

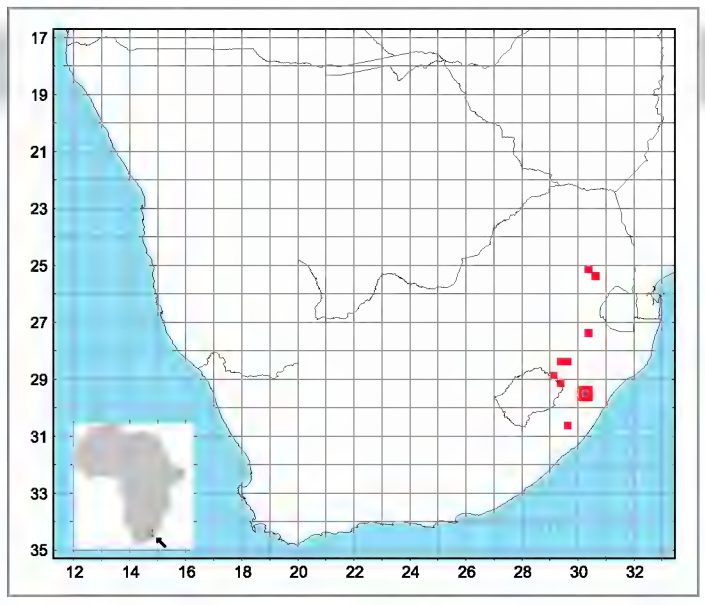
= *Caccobius* (*Diaglyptus*) *pluridens* d'Orbigny, 1905

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: *O. pauxillum*: 'prope fluvium Gariep' [near Orange River, South Africa, although female type labelled 'Caffraria']; *C. pluridens*: 'Nyassa' [type labelled: 'Mozam. Nyassa' = Mozambique].
Taxonomy: Accepted species.
Distribution: Recorded from scattered localities across southern African savanna into the E and NE tropics: South Africa, Zimbabwe, Mozambique, Kenya, Ethiopia.
Locality data (mean ± SD, range): Altitude: 924 ± 476, 64–1 383 m; annual rainfall: 629 ± 197, 306–852 mm; annual temperature (max. + min. /2): 20.1 ± 1.5, 18.9–22.1°C (N=5).
Habitat: No quantitative assessment; however, most of the few known southern African localities coincide with deep sands: E coast (Sodwana Bay); Southern African Bushveld (Nylsvlei, Boekenhoutskloof, Mmaboela Estate); Zimbabwean Miombo woodland (Harare).
Food types: No quantitative assessment; no records.
Temporal activity: Diel flight periodicity unknown, but probably diurnal like other *Odontoloma* species; active primarily during the summer rainy season (Oct. to Apr.).
Ecoregions Zimbabwe: Southern Miombo Woodlands (AT0719).
Bioregions South Africa: Central Bushveld (SVcb) (Savanna Biome); Indian Ocean Coastal Belt Biome (CB).
Assessment rationale: EOO = 1 021 280 km^2 (gross estimate); widespread EOO, but AOO likely smaller because of putative specialisation to sandy soils; recorded in high frequency on deep sands at Nylsvlei; assessed as Least Concern (LC) on basis of wide range, but essentially Data Deficient (DD).
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; protected at Nylsvlei Nature Reserve (South Africa).



Odontoloma peckorum

Howden & Scholtz, 1987

No synonyms

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'REP. SOUTH AFRICA: Natal, 75 km WSW Estcourt, Cathedral Peaks For. Sta.' [Cathedral Peak Forest Station, KwaZulu-Natal, South Africa].

Taxonomy: Accepted species.

Distribution: Moist upland or highland grassland along the edges of the NE escarpment, South Africa.

Locality data (mean ± SD, range): Altitude: 1 544 ± 463, 974–2 497 m; annual rainfall: 816 ± 52, 726–914 mm; annual temperature (max. + min. /2): 14.4 ± 2.3, 9.2–16.9°C (N=12).

Habitat: On an altitudinal transect in KwaZulu-Natal, sampled in grassland on sandy clay loam soils primarily at 1 500 and 1 900 m (11.9 or 19.8 per trap), uncommon at 1 000 (2.4), 2 400 (0.1) and 2 800 m (0.04).

Food types: No quantitative assessment; sampled to cattle dung baits.

Temporal activity: Diel flight periodicity unknown, but probably diurnal like other *Odontoloma* species; active during the summer rainy season (Oct. to Mar.).

Bioregions South Africa: E edges of Drakensberg Grassland (Gd), Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs) (Grassland Biome).

Assessment rationale: EOO = 19 885 km^2; wide range, primarily in grassland along NE escarpment where substantial local abundance is recorded at 1 500–1 900 m; large part of range at higher altitude under protection; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; protected in uKhahlamba Drakensberg Park (World Heritage Site).

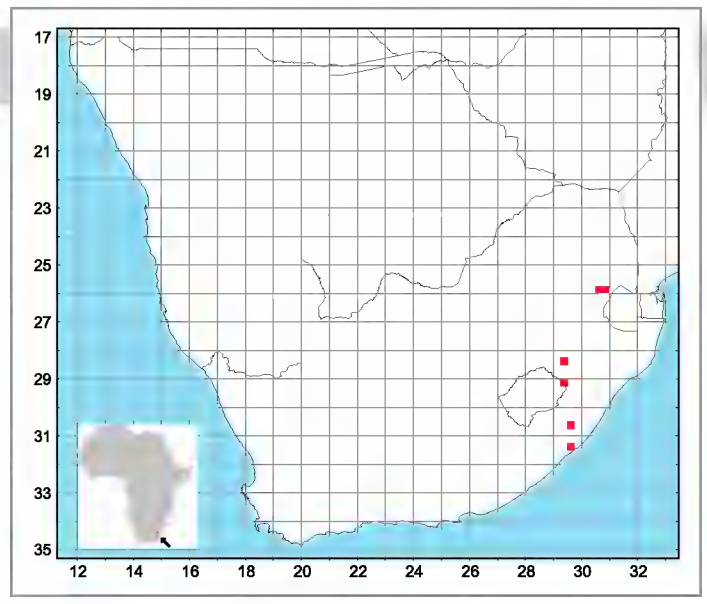
Odontoloma planatum

Howden & Scholtz, 1987

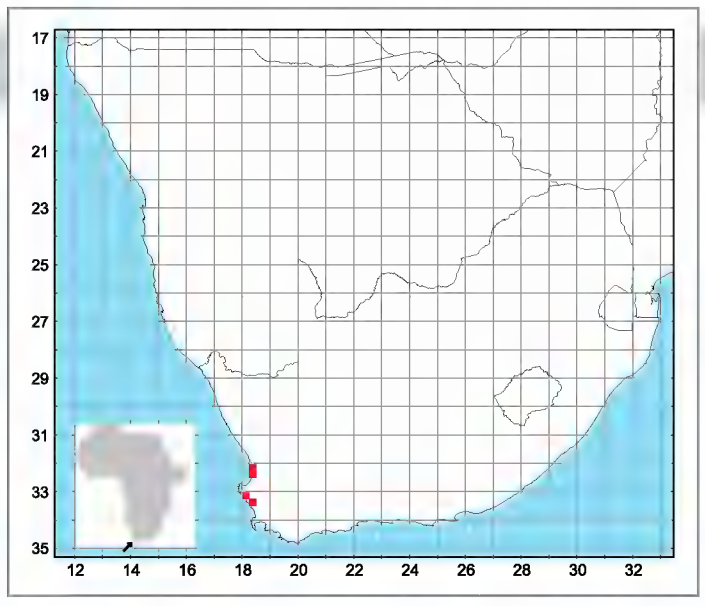
No synonyms

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: 'SOUTH AFRICA: Natal, 75 km WSW Estcourt, Cathedral Peaks For. Sta., 1400 m' [Cathedral Peak Forest Station, KwaZulu-Natal, South Africa].
Taxonomy: Accepted species.
Distribution: Mostly moist upland and coastal grassland along lower NE escarpment and SE coast, South Africa.
Locality data (mean ± SD, range): Altitude: 1 096 ± 811, 114–2 497 m; annual rainfall: 900 ± 140, 726–1 157 mm; annual temperature (max. + min. /2): 16.3 ± 3.5, 9.2–19.5°C (N=7).
Habitat: No quantitative assessment, no records.
Food types: No quantitative assessment, no records.
Temporal activity: Diel flight periodicity unknown, but probably diurnal like other *Odontoloma* species; active during the summer rainy season (Sept. to Feb.).
Bioregions South Africa: E edges of Drakensberg Grassland (Gd), Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs) (Grassland Biome); also Indian Ocean Coastal Belt Biome (CB).
Assessment rationale: EOO = 14 615 km^2; ecologically poorly known, but occupies a moderately large range so currently assessed as Least Concern (LC) although essentially Data Deficient (DD).
Conservation measures: Assessment of conservation status would be improved by quantitative ecological data; unclear whether or not it has been recorded from protected areas.



Odontoloma pusillum

Howden & Scholtz, 1987

No synonyms

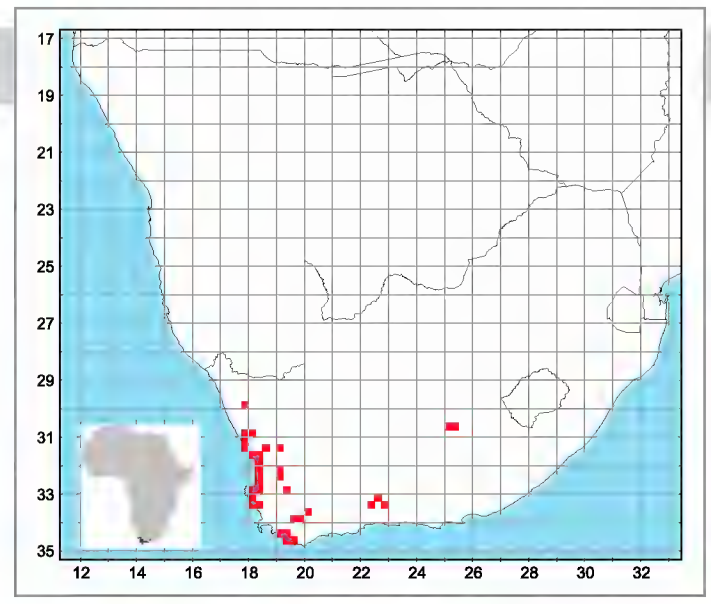
Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: '[S. AFRICA], S.W. Cape Prov., Langebaan (12 km SE Geelbek)' [Farm Geelbek, now in West Coast National Park].
Taxonomy: Accepted species.
Distribution: Dry west coastal deep sands of the SW Western Cape, South Africa.
Locality data (mean ± SD, range): Altitude: 94 ± 79, 31–199 m; annual rainfall: 273 ± 68, 191–350 mm; annual temperature (max. + min. /2): 16.6 ± 1.0, 15.7–17.9°C (N=5).
Habitat: On the West Coast: primarily recorded at farms on W coastal deep sands; at Geelbek: equally abundant in natural strandveld shrubland (550) and adjacent sparse grassland cleared of shrubs (530); at Pampoenvlei much more abundant in shrubland on deep sand (287) than on adjacent sandy loam (31).
Food types: No quantitative assessment; sampled to cattle dung in abundance.
Temporal activity: Diurnal flight activity; seasonal activity during the winter rainy season in autumn, winter and spring (Apr. to Oct.) with autumn (May) and spring peaks (Aug., Sept.).
Bioregions South Africa: West Strandveld (F 11) vegetation units: Langebaan Dune Strandveld (FS 5), Lamberts Bay Strandveld (FS 1); also Southwest Fynbos (FO 3), Atlantis Sand Fynbos (FFd 4) (all Fynbos Biome).
Assessment rationale: EOO = 1 685 km^2; possibly restricted to a small natural range in an area subject to extensive habitat transformation (FFd 4: 40%, FS 1: 25%, FS 5: 35%); on the basis of small EOO < 5 000 km^2 at only five locations; would qualify for an IUCN threat category of Endangered (EN), but on the basis of small body size and local abundance in a protected area with tolerance of vegetation transformation, currently tentatively assessed as Least Concern (LC).
Conservation measures: Assessment of conservation status would be improved by quantitative data on food type associations particularly in West Coast National Park as cattle have been removed from the type locality on the Farm Geelbek since the proclamation of the park; assumed to be protected within West Coast National Park.

Odontoloma pygidiale

Péringuey, 1901



No synonyms

Global: LC (see IUCN Red List – LC)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'Cape Colony (Cape Town, Stellenbosch, Paarl)' [Western Cape, South Africa].

Taxonomy: Accepted species, but Howden and Scholtz (1987) noted clinal differences in morphology, particularly in relative prominence of the elytral umbone, which is associated with relative wing development and may indicate a species complex; close to *O. pusillum* Howden & Scholtz, 1987 and *O. endroedyi* Howden & Scholtz, 1987.

Distribution: Disjunct pattern, which may or may not indicate more than one species; records mostly from dry to arid, lower-altitude parts of winter and bimodal rainfall regions plus NE edge of Karoo, South Africa.

Locality data (mean ± SD, range): Altitude: 334 ± 409, 1–1 408 m; annual rainfall: 243 ± 91, 108–448 mm; annual temperature (max. + min. /2): 16.8 ± 1.4, 13.2–19.2°C (N=47).

Habitat: No quantitative assessment; no records.

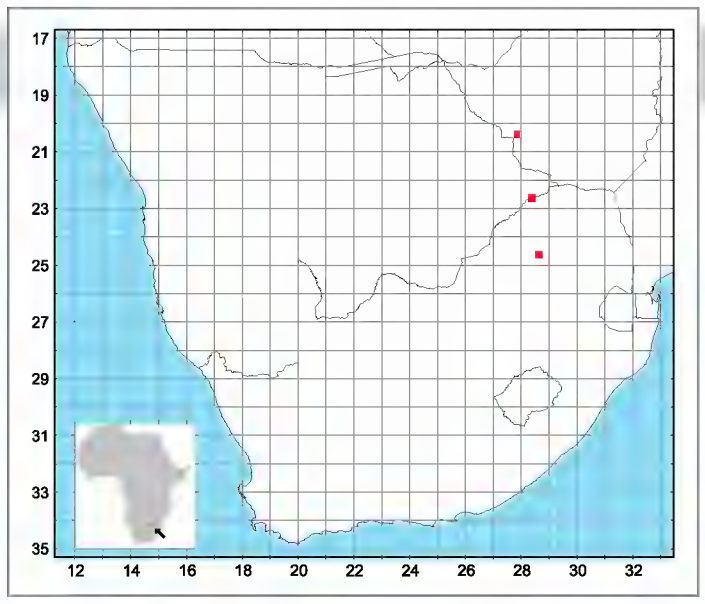
Food types: No quantitative assessment; no records.

Temporal activity: Diel periodicity unknown, but probably diurnal like other *Odontoloma* species; recorded during all months except mid-summer (Jan.), but most records in spring in the Western Cape and spring plus autumn in the Eastern Cape.

Bioregions South Africa: Primarily Namaqualand Hardeveld (SKn), Rainshadow Valley Karoo (SKv) (Succulent Karoo Biome); Northwest Fynbos (FO 1), Southwest Fynbos (FO 2) (Fynbos Biome); NE Upper Karoo (NKu) (Nama Karoo Biome).

Assessment rationale: EOO = 71 165 km^2; widespread in arid regions that are little transformed; probable that most populations are not threatened, so irrespective of questions on taxonomic identity, the species or species complex may be assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by (a) a taxonomic study to determine if *O. pygidiale* comprises a single species or a complex, and (b) quantitative data on ecological associations; currently no records from protected areas.



Odontoloma quadridens

(d'Orbigny, 1908)

No synonyms

Global: DD

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Caccobius* (*Diaglyptus*) *quadridens*: 'Rhodesia, Plumtree' [Plumtree, Zimbabwe].

Taxonomy: Accepted species revalidated by Howden and Scholtz (1987) after synonymy with *O. pauxillum* Boheman, 1857, by Janssens (1938a) and Ferreira (1969).

Distribution: Bushveld of the E Kalahari and its outlier patches: South Africa, Zimbabwe.

Locality data (mean ± SD, range): Altitude: 1 040 ± 321, 708–1 349 m; annual rainfall: 486 ± 156, 306–585 mm; annual temperature (max. + min. /2): 20.3 ± 1.5, 19.3–22.1°C (N=3).

Habitat: No quantitative assessment; the three known localities coincide with patches of deep sands.

Food types: No quantitative assessment; no records.

Temporal activity: Diel flight periodicity unknown, but probably diurnal like other *Odontoloma* species; active during the summer rainy season (Oct., Mar.).

Ecoregions Zimbabwe: Southern African Bushveld (AT0717).

Bioregions South Africa: Central Bushveld (SVcb) (Savanna Biome).

Assessment rationale: EOO = 15 205 km^2 (presumably underestimated); ecologically poorly known; occupies a large EOO, but AOO may be limited by soil specialisation, although this has not been supported quantitatively; currently assessed as Data Deficient (DD).

Conservation measures: Assessment of conservation status would be improved by quantitative ecological data and a survey to determine its full EOO and AOO; protected in Nylsvlei Nature Reserve.

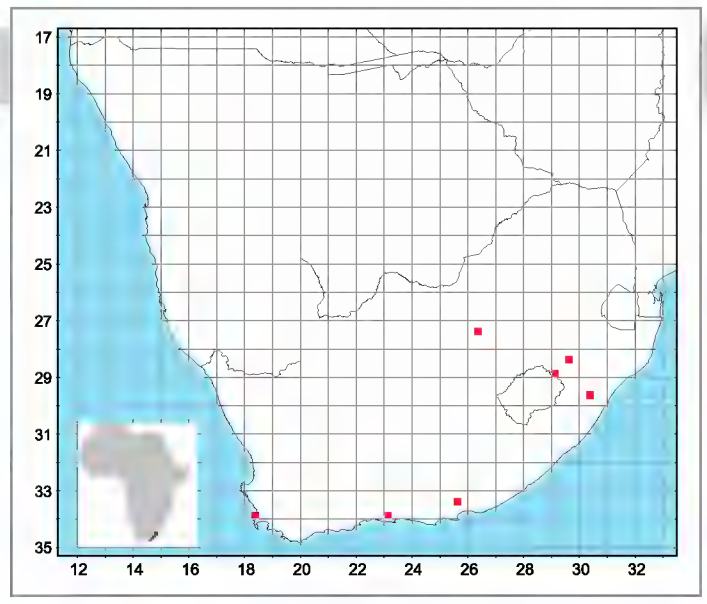
Odontoloma sculpturatum

(Harold, 1868a)

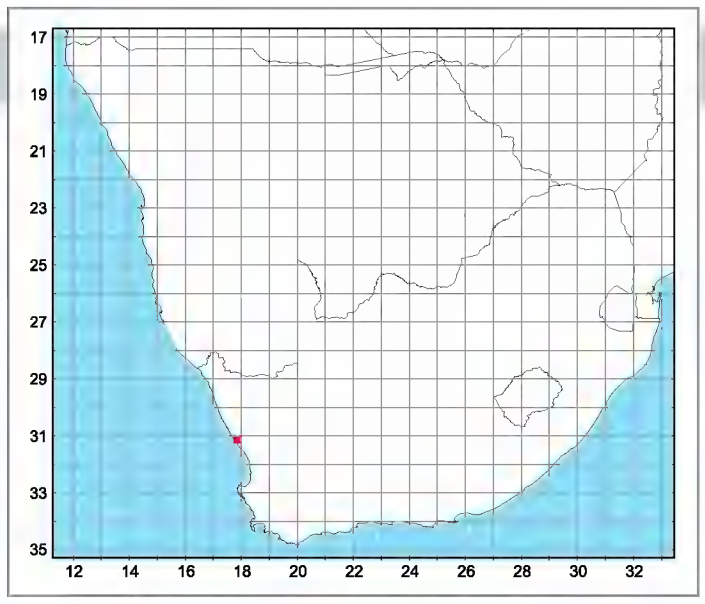
= *Caccobius* (*Diaglyptus*) *multifidus* d'Orbigny, 1908

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: As *Epirhinus sculpturatus*: 'Cap bon. spei' [Cape of Good Hope, South Africa], lectotype: 'Oranje, Burghisrd.' [South Africa]; *C. multifidus*: 'Colonie du Cap' [Cape Colony, South Africa].
Taxonomy: Accepted species.
Distribution: Widespread along the SE seaboard of South Africa from upland summer rainfall areas in the N to lowland winter and bimodal rainfall areas in the S.
Locality data (mean ± SD, range): Altitude: 861 ± 808, 93–1 371 m; annual rainfall: 597 ± 187, 392–858 mm; annual temperature (max. + min. /2): 16.3 ± 2.7, 10.6–18.7°C (N=7).
Habitat: No quantitative assessment; no records but N distribution primarily in grassland regions.
Food types: No quantitative assessment; no records.
Temporal activity: Diel flight periodicity unknown, but probably diurnal like other *Odontoloma* species; active primarily during spring and the summer rainy season in the N (Sept. to Apr.).
Bioregions South Africa: Dry Highveld Grassland (Gh), Drakenberg Grassland (Gd), Sub-Escarpment Grassland (Gs) (Grassland Biome); Sub-Escarpment Savanna (SVs) (Savanna Biome); Albany Thicket Biome (AT); Southwest and Eastern Fynbos (FO 2, FO 6).
Assessment rationale: EOO = 64 415 km^2 (gross estimate); widespread across climatically different areas, but ecologically poorly known; therefore assessed as Data Deficient (DD).
Conservation measures: Before conservation status may be assessed a survey is required to improve distributional data (EOO, AOO) and provide quantitative ecological data; not currently known from any nature reserve.



Odontoloma spinicaudum

Howden & Scholtz, 1987

No synonyms

Global: DD
Endemic: RSA

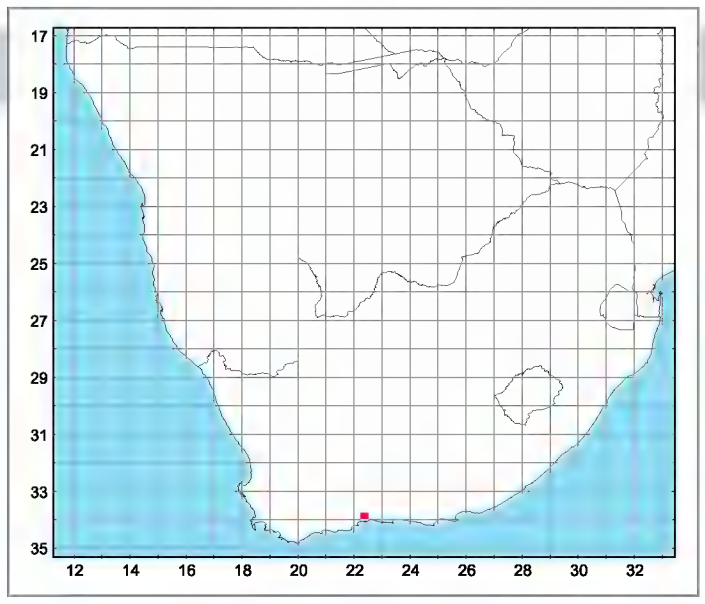
J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'S. AFRICA: Namaqualand, Klein Kogel Fontein' [farm in Namaqualand, South Africa].
Taxonomy: Accepted species.
Distribution: Known from only the type locality on the arid West Coast sandveld, South Africa.
Locality data (average): Altitude: 38 m; annual rainfall: 142 mm; annual temperature (max. + min. /2): 18.2°C (N=1).
Habitat: No quantitative assessment; recorded in a area of deep sands where the natural vegetation is coastal shrubland.
Food types: No quantitative assessment; no records.
Temporal activity: Wings obsolete; diel periodicity unknown, but probably diurnal like other *Odontoloma* species; recorded in spring during the winter rainy season (Aug.).
Bioregions South Africa: Vegetation unit: Namaqualand Strandveld (SKs 7) (Namaqualand Sandveld Bioregion, Succulent Karoo Biome).
Assessment rationale: EOO unknown; known only by the single female holotype; conservation status impossible to determine in absence of range and ecological data; assessed as Data Deficient (DD).
Conservation measures: Before conservation status may be assessed, it is necessary to survey the sandveld around Klein Kogel Fontein and obtain quantitative ecological data; not known from any protected area.

Genus *Outenikwanus* Scholtz & Howden, 1987

Type species and designation: *Outenikwanus tomentosus* Scholtz & Howden, 1987, by original designation.
Synonyms: None.
Last review: Genus created by Scholtz and Howden (1987).

Outenikwanus Scholtz & Howden, 1987, is small-bodied, flightless and monotypic. It has been recorded from leaf litter of a single Southern Afrotemperate Forest patch (FOz 1) on mountains along the S seaboard of the Eastern Cape, South Africa. It has been assessed as Data Deficient (DD) although the combined area of upland patches of FOz 1 would probably be sufficiently small to justify an assessment of Vulnerable (VU).



Outenikwanus tomentosus

Scholtz & Howden, 1987

No synonyms

Global: DD
Endemic: RSA

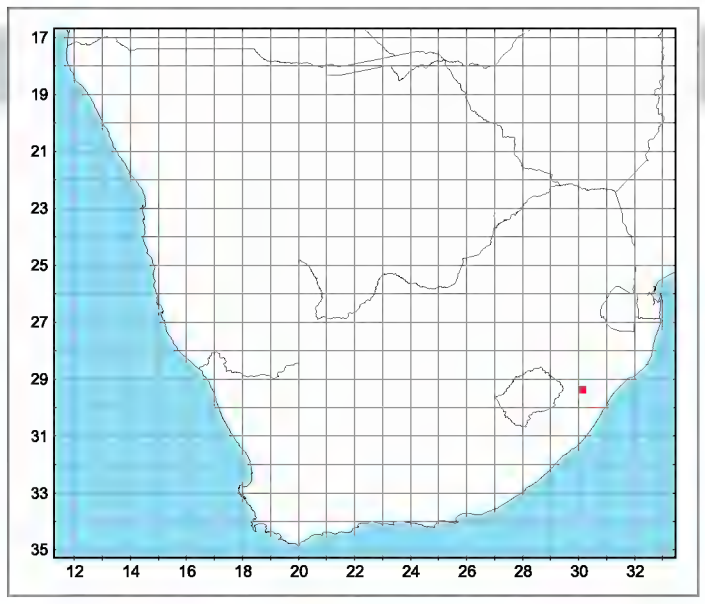
J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'S. Cape Mts., Outenikwa Pass' [Eastern Cape, South Africa].
Taxonomy: Accepted species.
Distribution: Currently known only from an indigenous forest patch adjoining the Outeniqua Pass, Outeniqua Mountains.
Locality data (average): Altitude: 999 m; annual rainfall: 404 mm; annual temperature (max. + min. /2): 13.8°C (N=1).
Habitat: No quantitative assessment; recorded from leaf litter of indigenous forest.
Food types: Not known.
Temporal activity: Flightless, diel periodicity unknown; recorded during early summer (Nov., Dec.) in the bimodal rainfall region (spring, autumn peaks).
Bioregions South Africa: Southern Afrotemperate Forest (FOz 1) (Forest Biome).
Assessment rationale: EOO uncertain; currently, only known by the type series and a few other individuals, all recorded in forest on the Outeniqua Pass; nothing else known concerning EOO, AOO and ecological habits; currently assessed as Data Deficient (DD).
Conservation measures: EOO, AOO and conservation status may only be assessed after a survey of the many small scattered upland patches of Afrotemperate indigenous forest between Mossel Bay and Jeffreys Bay in the S Cape; a gradsect from grassland into forest patches would confirm the vegetation specialisation and restricted AOO; currently only known to be protected within Witfontein Nature Reserve on the Outeniqua Pass.

Genus *Parvuhowdenius* Deschodt & Scholtz, 2008

Type species and designation: *Parvuhowdenius harrisoni* Deschodt & Scholtz, 2008, by original designation.
Synonyms: None.
Last review: Genus created by Deschodt and Scholtz (2008).

Parvuhowdenius Deschodt & Scholtz, 2008, is small-bodied, flightless and monotypic. Known only from litter in a single small patch of Southern Mistbelt Forest. The patch occurs at higher altitude than those supporting the genus, *Nebulasilvius* Deschodt & Scholtz, 2008. Given the very small known range and limited ecological data, *Parvuhowdenius* is assessed as Data Deficient (DD), although an alternative assessment as Vulnerable (VU) is probably justified.



Parvuhowdenius harrisoni

Deschodt & Scholtz, 2008

No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

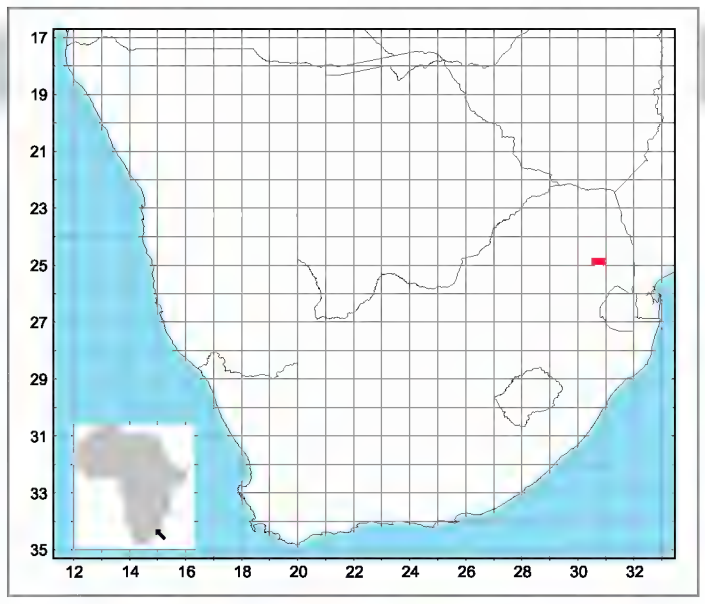
Type locality: 'Karkloof For. 1 300 m' [Karkloof Forest, KwaZulu-Natal, South Africa].
Taxonomy: Accepted species.
Distribution: Monotypic genus currently known only from the type locality: Karkloof Forest.
Locality data (average): Altitude: 1 364 m; annual rainfall: 855 mm; annual temperature (max. + min. /2): 14.7°C (N=1).
Habitat: No quantitative assessment; all known specimens sifted from forest leaf litter; assumed to be a forest specialist.
Food types: Not known.
Temporal activity: Flightless; diel periodicity unknown; recorded during the summer rainy season (Dec.).
Bioregions South Africa: Southern Mistbelt Forest (FOz 3) (Forest Biome).
Assessment rationale: EOO = 16.9 km^2 (size of Karkloof Forest patch in which *P. harrisoni* was recorded); currently known by only three individuals from a single privately owned forest patch that is under significant threat; deserves at least Vulnerable (VU) status, but so poorly known, assessed as Data Deficient (DD).
Conservation measures: Before an assessment of conservation status may be made, it is necessary to determine its full EOO and population density by conducting a further survey of Karkloof Forest and many other nearby fragments of FOz 3; a gradsect from forest fragments into grassland would confirm its limited AOO due to vegetation specialisation; protected by the Karkloof Conservancy comprising landowners, conservation and forestry organisations.

As published in Deschodt & Scholtz (2008).

Genus *Peckolus* Scholtz & Howden, 1987

Type species and designation: *Peckolus parvus* Scholtz & Howden, 1987, by original designation.
Synonyms: None.
Last review: Genus created by Scholtz and Howden (1987); new species added by Howden and Scholtz (1988), Deschodt and Scholtz (2008).

Peckolus Scholtz & Howden, 1987, currently comprises three species from small Northern Mistbelt or Northern Afrotemperate forest patches along the upper edge of the NE escarpment of South Africa. Although all three species are assessed as Data Deficient (DD), the rarity of collection and small putative EOO and AOO would deserve IUCN threat categories of at least Endangered (EN), pending thorough surveys of other forest patches.



Peckolus alpinus

Howden & Scholtz, 1988

No synonyms

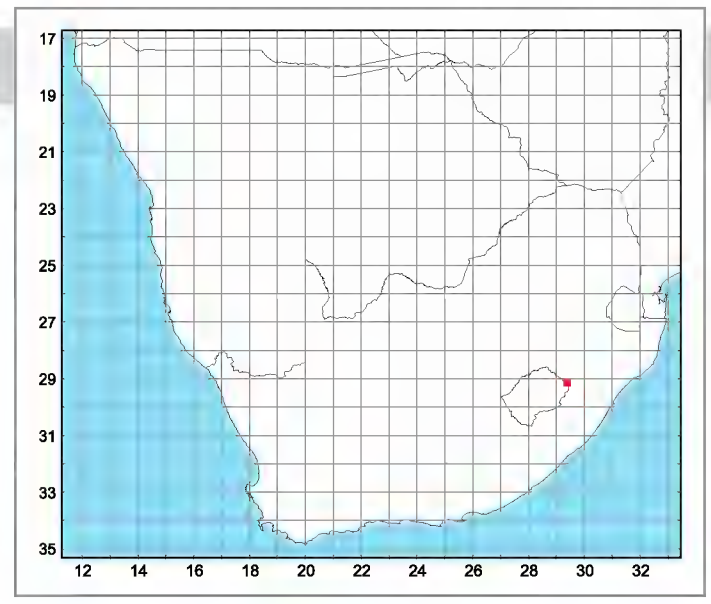
Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'South Africa, Transvaal, 11 km S.E. Pilgrims Rest, 1 500 m' [Mpumalanga, South Africa].
Taxonomy: Accepted species.
Distribution: Localised on upper edge of E escarpment within the northernmost of three discrete blocks of FOz 4 forest patches forming the Mpumalanga Mistbelt Forest Region, South Africa.
Locality data (mean ± SD, range): Altitude: 1 647 ± 218, 1 493–1 800 m; annual rainfall: 961 ± 4, 958–963 mm; annual temperature (max. + min. /2): 14.6 ± 1.3, 13.7–15.5°C (N=2).
Habitat: No quantitative assessment; observed in ravines supporting patches of relict forest with well-developed leaf litter.
Food types: No quantitative assessment; sampled to carrion.
Temporal activity: Flightless; diel periodicity unknown; recorded in the summer rainy season (Dec.).
Bioregions South Africa: Northern (Limpopo) division of Northern Mistbelt Forest (FOz 4) (Forest Biome).
Assessment rationale: EOO = 15 km^2; current known forest AOO = 4.8 km^2 (both presumably underestimated); probably occurs in numerous other larger, nearby forest patches that remain unsurveyed; the FOz 4 vegetation unit is cited as poorly protected, but not currently threatened; species assessed as Data Deficient (DD) since range and ecological habits are poorly known; however, would currently deserve an IUCN threat category of at least Endangered (EN) on basis of AOO < 500 km^2 at < 5 known localities.
Conservation measures: For the conservation of this species, it would be essential to protect the block of FOz 4 forest patches found on the escarpment edge between Sabie and Klaserie; to determine the EOO, it would be necessary to survey the high altitude FOz 4 forest patches along the entire NE edge of the escarpment in Mpumalanga and Limpopo; a gradsect from grassland into forest patches would confirm the vegetation specialisation and restricted AOO; protected in the private Mt Sheba Nature Reserve.

Peckolus parvus

Scholtz & Howden, 1987

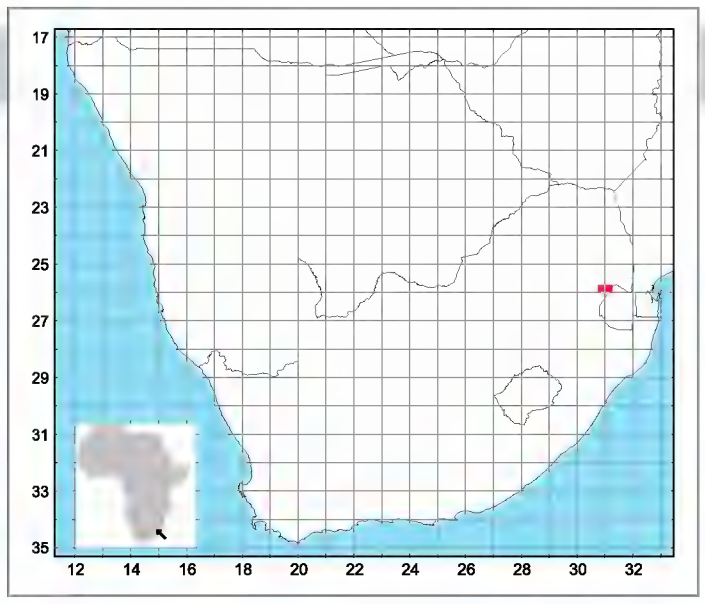


No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Natal, 75 m WSW Estcourt, Cathedral Peaks For. Sta.' [South Africa].
Taxonomy: Accepted species.
Distribution: Known only from a single high altitude locality on the E escarpment of South Africa on the NE border of Lesotho.
Locality data (average): Altitude: 2 497 m; annual rainfall: 810 mm; annual temperature (max. + min. /2): 9.2°C (N=1).
Habitat: No quantitative assessment; observed in high altitude (1 800 m) podocarp forest litter containing moss and fungal hyphae; probably a forest specialist.
Food types: Not known.
Temporal activity: Flightless; diel periodicity unknown; recorded during the summer rainy season (Dec.).
Bioregions South Africa: Northern Afrotemperate Forest (FOz 2) (Forest Biome).
Assessment rationale: EOO = 1.4 km^2 (presumably underestimated; comprises area of type locality, forest patch); range and ecological habits poorly known; therefore, assessed as Data Deficient (DD); the small known AOO of < 500 km^2 at < 5 locations would deserve an IUCN threat category of at least Endangered (EN); however, the single patch of montane forest from which it is known, occurs within a protected area containing other similar forest patches; therefore, despite minute known range, possibly not currently under serious threat.
Conservation measures: Continuing protection of FOz 2 forest patches would be essential for the conservation of this species; to determine the EOO, it is necessary to conduct a survey of the many other FOz 2 forest patches that occur along the W border of KwaZulu-Natal adjoining Lesotho, Free State and Mpumalanga; a gradsect from grassland into forest patches would confirm the vegetation specialisation and restricted AOO; protected in the uKhahlamba Drakensberg Park (World Heritage Site).



Peckolus poenskopius

Deschodt & Scholtz, 2008

No synonyms

Global: DD
Endemic: RSA

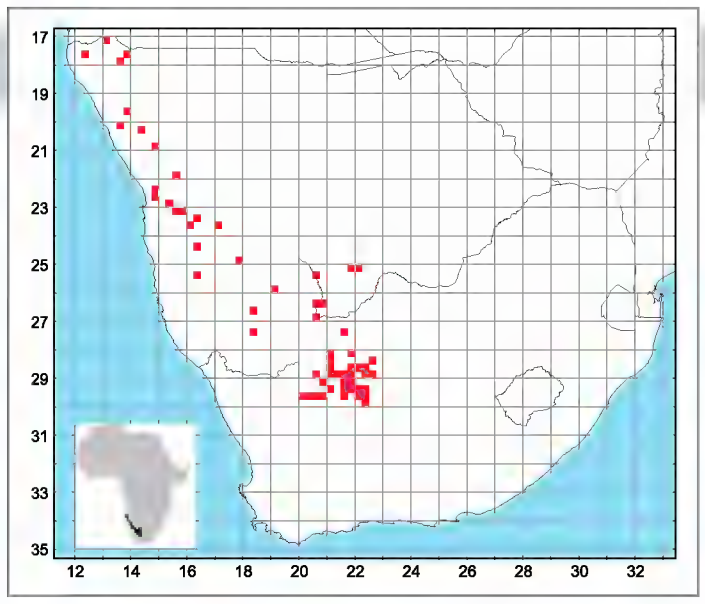
J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Nelshoogte, Knuckles rocks for.' [Forest near Knuckles Rocks, Mpumalanga, South Africa].
Taxonomy: Accepted species.
Distribution: Localised on E escarpment within the southernmost of three discrete blocks of FOz4 forest patches forming the Mpumalanga Mistbelt Forest Region, South Africa.
Locality data (mean ± SD, range): Altitude: 1 085 ± 224, 831–1 257 m; annual rainfall: 1 005 ± 137, 892–1 157 mm; annual temperature (max. + min. /2): 18.0 ± 1.4, 17.0–19.6°C (N=3).
Habitat: No quantitative assessment; recorded in wet forest litter.
Food types: Not known.
Temporal activity: Flightless; diel periodicity unknown; recorded in the summer rainy season (Feb.).
Bioregions South Africa: Southern (Mpumalanga) division of Northern Mistbelt Forest (FOz 4) (Forest Biome).
Assessment rationale: EOO = 85 km^2 (presumably underestimated); may occur in numerous other nearby forest patches that remain unsurveyed; the FOz 4 vegetation unit is cited as poorly protected, but not currently threatened; species assessed as Data Deficient (DD) since range and ecological habits are poorly known; however, current known EOO of < 5 000 km^2 at < 5 locations would deserve an IUCN threat category of at least Endangered (EN).
Conservation measures: For the conservation of this species, it would be essential to protect the block of FOz 4 forest patches found on the escarpment near the Eswatini border between Barberton and Malelane; to determine the EOO, it would be necessary to survey the lower-altitude FOz 4 forest patches along the entire NE edge of the escarpment in Mpumalanga and Limpopo; a gradsect from grassland into forest patches would confirm the vegetation specialisation and restricted AOO; protected in Nelshoogte and Josephdal nature reserves.

Genus *Pycnopanelus* Arrow, 1931

Type species and designation: *Pycnopanelus rotundus* Arrow, 1931, by original designation.
Synonyms: None.
Last review: Genus created by Arrow (1931); African species reviewed by Scholtz and Howden, (1987).

Pycnopanelus Arrow, 1931, currently comprises three species with disjunct distributions in the Afrotropical (2) and W Oriental regions (India: 1). The Indian species is represented only by the type specimen. The African species have been recorded from arid regions in the SW and NE (Sudan: two specimens). The SW species from the arid late summer rainfall region of Namibia, Botswana and South Africa is known by many individuals and is assessed as Least Concern (LC). Scholtz and Howden (1987) express their doubts that *Pycnopanelus* belongs with the Canthonini (see placement in the phylogeny of Tarasov and Dimitrov (2016)).



Pycnopanelus krikkeni

Cambefort, 1978

No synonyms

Global: LC
Endemic: RSA, Botswana, Namibia

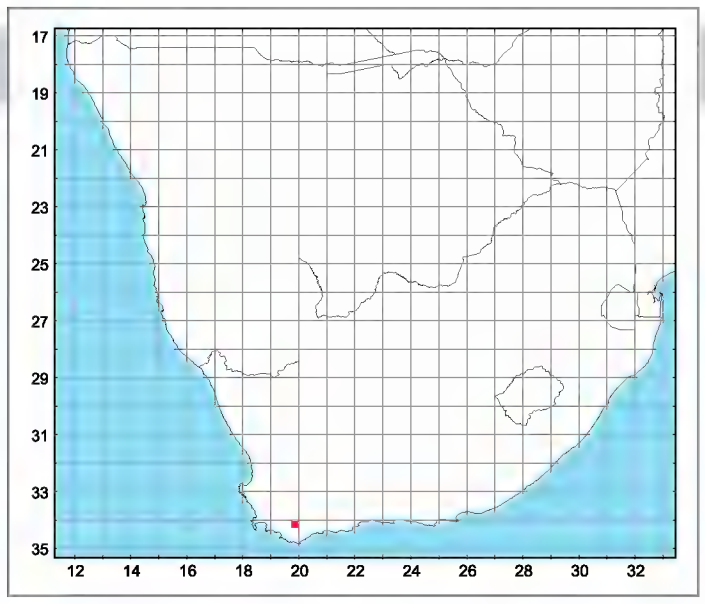
J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Noachebeb, 27 mls NNE Grunau' [S Namibia].
Taxonomy: Accepted species.
Distribution: Warmer parts of the arid late summer rainfall region from South Africa across SW Botswana and W Namibia; probably also SW Angola, but no known records.
Locality data (mean ± SD, range): Altitude: 987 ± 208, 361–1 782 m; annual rainfall: 191 ± 65, 39–423 mm; annual temperature (max. + min. /2): 18.8 ± 1.2, 15.8–21.3°C (N=110).
Habitat: In Northern Cape: high frequency of records in warmer, arid areas, especially Bushmanland (5.7/trap at 91% of 67 study sites) on sand (3.8/trap), loamy sand (6.1), sandy loam (2.3), sandy clay loam (0.7); DBRU collection records from sand (4), sandy loam (1) in grassland (1), scrub/shrubland (3), open woodland (1).
Food types: No quantitative assessment; DBRU collection records from dung of cattle (2), donkey (1); sampled in large numbers to composite sheep/cattle dung baits.
Temporal activity: Diel flight periodicity unknown, possibly diurnal; recorded during the late summer rainy season (Jan. to Apr.) and in the winter dry season in central Namibia (June, July).
Ecoregions Namibia, Botswana: NW Nama Karoo (AT1314), SW Kalahari Xeric Savanna (AT1309), Namibian Savanna Woodlands (AT1316).
Bioregions South Africa: Low-altitude N Bushmanland (NKb) (Nama Karoo Biome) with representation in the Kalahari Duneveld (SVk) (Savanna Biome).
Assessment rationale: EOO = 264 500 km^2; does not face any threats due to widespread distribution across an arid area used primarily for conservation or the grazing of domestic livestock whose dung it readily colonises; transformation: close to 0% (both NKb and SVk); assessed as Least Concern (LC).
Conservation measures: Assessment of conservation status would benefit from further quantitative ecological data, particulartly food associations; protected in Kgalagadi Transfrontier Park (Botswana, South Africa) and inland margin of the Namib-Naukluft Park (Namibia).

Genus *Silvaphilus* Roets & Oberlander, 2010

Type species and designation: *Silvaphilus oubosiensis* Roets & Oberlander, 2010, by original designation.
Synonyms: None.
Last review: Genus created by Roets and Oberlander (2010).

Silvaphilus Roets & Oberlander, 2010, is small-bodied, flightless and monotypic. It has been recorded from dung and leaf litter of a single Southern Afrotemperate Forest patch (FOz 1) on mountains along the S seaboard of the Western Cape, South Africa. By virtue of extremely small known range on private land, it currently deserves an assessment of Vulnerable (VU) or even Endangered (EN).



Silvaphilus oubosiensis

Roets & Oberlander, 2010

No synonyms

Global: VU
Endemic: RSA

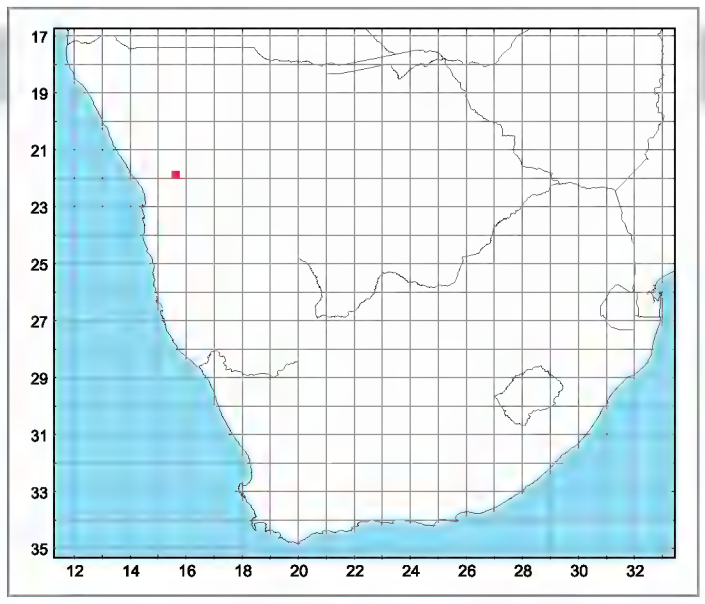
J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Western Cape Province, Riviersonderend, Oubos Forest' [South Africa].
Taxonomy: Accepted species.
Distribution: Known only from Oubos Forest, Riviersonderend Mountains, Western Cape, South Africa.
Locality data (average): Altitude: 389 m; annual rainfall: 367 mm; annual temperature (max. + min. /2): 16.3°C (N=1).
Habitat: No quantitative assessment; recorded only within forest after a search of herbivore dung both outside and inside forest habitat; also found in leaf litter and in top 10 mm of soil under dung.
Food types: No quantitative assessment; recorded under fresh mammalian dung, both herbivore pellets and an insectivore dropping; not recorded under old dung.
Temporal activity: Flightless; diel periodicity unknown; recorded in late spring at end of winter rainy season (Nov.).
Bioregions South Africa: Southern Afrotemperate Forest (FOz 1) (Forest Biome).
Assessment rationale: EOO 6 km^2 (estimated); AOO = 1.6 km^2 (Oubos Forest); only known from a single small, privately owned forest patch in an isolated mountain range where only one other even smaller forest patch occurs (0.7 km^2); owing to the extremely small potential EOO and AOO in few locations, this species would qualify for at least Vulnerable (VU) status, possibly even Endangered (EN).
Conservation measures: A survey is required to determine if this monotypic genus might occur in any of the other few patches of Southern Afrotemperate Forest found in the Western Cape or if it is endemic to the Riviersonderend Mountains; however, owing to its isolation, it seems likely that protection of Oubos Forest and the only other forest patch in this mountain range would be essential for the conservation of *S. oubosiensis*; Oubos Forest is conserved by the owners.

Genus *Versicorpus* Deschodt, Davis & Scholtz, 2011

Type species and designation: *Versicorpus erongoensis* Deschodt, Davis & Scholtz, 2011, by original designation.
Synonyms: None.
Last review: Entire genus reviewed by Deschodt and Davis (2017).

Versicorpus Deschodt, Davis & Scholtz, 2011, now comprises two species from arid mountain blocks in Namibian Savanna Woodlands, Central Namibia, after a second species was added to *V. erongoensis* Deschodt, Davis & Scholtz, 2011, following transferral from *Namakwanus* Scholtz & Howden, 1987 (Deschodt & Davis 2017). As both species are known by only the holotype specimens, they are assessed as Data Deficient (DD) with no further speculative assessment; both type localities occur on private, but little-transformed, farm rangeland. One new species has been recently described from the Brandberg, Namibia (Deschodt & Sole 2019).



Versicorpus erongoensis

Deschodt, Davis & Scholtz, 2011

No synonyms

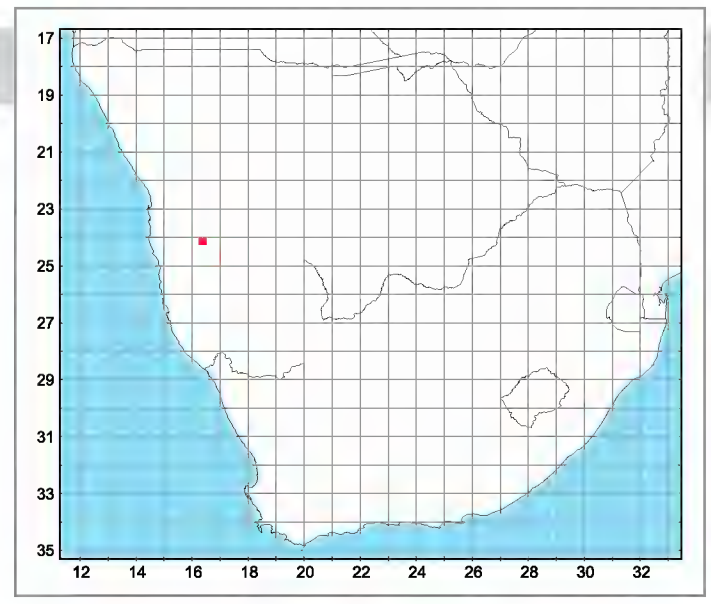
Global: DD
Endemic: Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'S.W.AFR. [Namibia], ErongoMT [Mountains]., Farm Amieb' [Farm Ameib, Erongo Mountains, Namibia].
Taxonomy: Accepted species.
Distribution: Known only by a single individual from the Erongo Mountains, Namibia.
Locality data (average): Altitude: 1 197 m; annual rainfall: 210 mm; annual temperature (max. + min. /2): 17.5°C (N=1).
Habitat: Unknown; holotype found under a stone.
Food types: Unknown.
Temporal activity: Flightless; diel periodicity unknown; recorded during the late summer rainy season (Feb.).
Ecoregions Namibia: Namibian Savanna Woodlands (AT1316).
Assessment rationale: EOO unknown; little ecological data recorded with the single known individual (holotype female); assessed as Data Deficient (DD).
Conservation measures: To assess conservation status, a survey is required of the Erongo Mountains and nearby highlands; this should determine the EOO, AOO and ecological associations; not currently known to be protected in any reserve.

Versicorpus streyi

(Frolov, 2005)



No synonyms

Global: DD (see IUCN Red List – DD as *Namakwanus streyi*)
Endemic: Namibia

| J | A | S | O | N | D | J | F | M | A | M | J |

Type locality: As *Namakwanus streyi*: 'Bullspoort [Bullsport 16°22'E 24°8'S], S.W.A.' [farm in Namibia].
Taxonomy: Accepted species.
Distribution: Known only from the somewhat inexact type locality in arid mountains of S Namibia (possibly Remhoogte Mts).
Locality data (average): Altitude: 1 621 m; annual rainfall: 179 mm; annual temperature (max. + min. /2): 15.9°C (N=1).
Habitat: Unknown.
Food types: Unknown.
Temporal activity: Flightless; diel and seasonal periodicity unknown.
Ecoregions Namibia: Namibian Savanna Woodlands (AT1316).
Assessment rationale: EOO unknown; extremely poorly known species; known only by a single individual (holotype male); no ecological data available; assessed as Data Deficient (DD).
Conservation measures: A survey is required to determine the EOO, AOO plus ecological associations and to assess conservation status; possibly protected within the Naukluft part of Namib-Naukluft National Park.

TRIBE COPRINI

Leach, 1815

As Coprides: Type genus: *Copris* Geoffroy, 1762.

Synonyms:

= Pinotinae Kolbe, 1905; Type genus: *Pinotus* Erichson, 1847b [=*Dichotomius* Hope, 1838, senior name] (but see Tarasov and Dimitrov 2016).

= Coptodactylini Paulian, 1933: Type genus *Coptodactyla* Burmeister, 1846.

= Dichotomiini Perreira, 1954: Type genus: *Dichotomius* Hope, 1838 (but see Tarasov and Dimitrov 2016).

Although they were listed as synonyms of the tribe Ateuchini by Bouchard et al. (2011), the recently named tribe Dichotomiini and older Pinotinae are here listed as synonyms of the Coprini to which the type genus, *Dichotomius* [= syn. *Pinotus*] and other *Copris*-like genera were transferred by the morphological phylogeny of Montreuil (1998). However, this synonymy would be superseded by the recent partial tribal revision of Tarasov and Dimitrov (2016), which has defined the Neotropical and Nearctic *Dichotomius* lineage as Dichotomiini *sensu novo*.

As defined by Montreuil (1998), the tribe Coprini is represented globally within areas of tropical or warm temperate climate. At the present time, 19 genera may be assigned to the tribe according to morphological criteria (14 with morphological phylogenetic support). These occur in three biogeographical centres (Afro-Eurasia: 12; Americas: 6; Australia/New Guinea: 2) with *Copris* Geoffroy, 1762, shared between Afro-Eurasia and the Americas. However, molecular phylogenies show that the tribal membership (as defined by Montreuil 1998) is polyphyletic with six distantly related lineages (Monaghan et al. 2007; Tarasov & Dimitrov 2016) in just 42% (8) of the genera (Monaghan et al. 2007). As a result, Tarasov and Dimitrov (2016) redefine a single lineage (genera: *Copris*, *Litocopris*) as Coprini *sensu novo*. All other coprine genera are awarded the status of *incertae sedis*. Under these circumstances the old tribal classification system is used in this book pending a full revision.

In the old sense, a total of 11 genera have been recorded for the Coprini in the Afrotropical region although some of these have recently (Marchisio & Zunino 2012) been claimed to be synonyms of *Copris* (see generic account for *Litocopris* Waterhouse, 1891). Hypothesised relationships differ between molecular phylogenies. Monaghan et al. (2007) indicate at least three distantly related lineages: **(1)** the basally derived *Macroderes* Westwood, 1842; **(2)** *Copris* plus *Heliocopris* Hope, 1837; and **(3)** the more terminally derived *Catharsius* Hope, 1837, plus *Metacatharsius* Montreuil, 1998 (but see discussion on authorship under generic account for *Metacatharsius*).

The recent partial tribal revision of Tarasov and Dimitrov (2016) also indicates at least three to four distantly related groupings of lineages, but suggests that none are basally derived. In rank order of derivation, these are: **(1)** *Copris* plus *Litocopris* now termed Coprini *sensu novo*; **(2)** *Catharsius* and *Metacatharsius*; with **(3)** *Heliocopris* in a neighbouring clade; **(4)** *Xinidium* Harold, 1869a, with *Macroderes* in a neighbouring clade. Subsequent to the preparation of this book in 2017, *Catharsius* and *Metacatharsius* have been transferred to the new tribe, Catharsiini by Takano (2018) although this transfer currently remains unpublished. Here, these genera and all three lineages remain included as *incertae sedis* in the tribe Coprini (old sense).

All three of these lineages are represented in Botswana, Namibia and/or South Africa where a total of seven genera are found.

(1A) *Copris* Geoffroy, 1762: Widely distributed genus in the Americas and Afro-Eurasia; represented by 33 southern African species centred primarily on winter and bimodal rainfall (6), Kalahari (3), upland grassland (7), E forest or grassland (3) or savanna (14) regions.

(1B) *Litocopris* Waterhouse, 1891: Species-poor Afrotropical genus; represented in South Africa by two species with SE or E seaboard distributions.

(2A) *Catharsius* Hope, 1837: Widely distributed genus in the Afrotropical and Oriental regions represented by 16 southern African species in upland grasslands (4), Kalahari (2), E forests and grasslands (2) and savannas (8).

(2B) *Metacatharsius* Montreuil, 1998 (but see discussion on authorship under generic account for *Metacatharsius*): Widely distributed genus found primarily on sandy soils in the Afrotropical region; represented by 11 validated southern African species centred mainly in the Kalahari (4), Kalahari/Namib (1), Kalahari/Namib/savanna (3), Kalahari/savanna (2) or SW Arid (1) regions.

(3) *Heliocopris* Hope, 1837: Widely distributed genus in the Afrotropical and Oriental regions represented by seven southern African species primarily found in arid to moist savannas.

(4A) *Macroderes* Westwood, 1842: Flightless genus comprising 14 species endemic to winter and bimodal rainfall regions, South Africa, after the revision of Frolov and Scholtz (2004). Further species were described by Abdalla et al. (2018) after the completion of this book (no species accounts presented here, but see Preamble).

(4B) *Xinidium* Harold, 1869a: Species-poor genus restricted to grassland and forest of the SE African highlands; represented by three South African species.

In the old sense, Coprini comprise medium to large-bodied, tunnelling taxa, some of which are known to construct brood ovoids within subterranean chambers. Most taxa do not currently face serious threats. However, two flightless *Copris* species are assessed as Endangered (EN) due to extreme habitat loss on the S coast in the winter and bimodal rainfall regions of South Africa. The poorly known flightless genus, *Macroderes*, may also face threats due to small species ranges, particularly those with more southerly occurrence where habitat transformation is greater.

Genus *Catharsius* Hope, 1837

Type species and designation: *Scarabaeus molossus* Linnaeus, 1758, by original designation (Hope 1837).
Synonyms: None.
Last review: Afrotropical species reviewed by Ferreira (1960a, 1960b) with a few new species described subsequently (Ferreira 1962a, 1963, 1971; Josso & Prévost 2009b; Josso 2011); recent review of a species group (Moretto 2008) and a discussion of Harold's types (Génier & Josso 2016); revision of entire genus (Takano, *pending publication*).

Catharsius Hope, 1837, was described as a subgenus of *Copris* Geoffroy, 1762 and has subsequently been raised to generic level. There is no phylogeny for the genus and although it clearly comprises a number of lineages, there has been no formal division into species groups. It currently comprises *circa* 100 valid species, most of which are Afrotropical (approx. 85) with fewer in the Oriental region (14) and one shared between the Afrotropical and Palaearctic (Egypt) regions. Takano (2018) has reviewed the genus and a number of name changes plus reassessments of synonyms are pending publication (indicated in species accounts).

Catharsius species are large to very large bodied. All species are macropterous and fly in darkness. They are considered to show similarities in behaviour to *Copris* in that dung is first buried at the end of a shallow tunnel and then relocated to a deeper tunnel. However, *Catharsius* species construct single brood balls per chamber. These are placed in series along the tunnel or adjacent at the tip of the tunnel. As this nesting strategy requires large amounts of dung, *Catharsius* are mostly found in moister regions together with large herbivores and their large droppings.

Of 16 species with valid names found in southern Africa, 12 are restricted to the region with three showing wider distributions. Some occur primarily on sandy soils, others on finer-grained soils. There seems to be a strong bias to carrion, omnivore and monogastric herbivore dung unlike in *Copris*. Three are specialists on monogastric herbivore dung.

In southern Africa, distributions of three species are centred on N Highveld Grassland (2) or on Highveld Grassland and Upper Karoo (1). However, most species show savanna distributions. Two are centred on the deep sands of the Kalahari, one a carrion specialist, the other biased to omnivore and monogastric herbivore dung. Two others are centred on the deep E coastal sands of Maputaland, one in grassland, one in forest. Some are centred across the savanna belt and beyond into the Kalahari (1) or onto the Highveld and S coast (1). Some are restricted to just savanna from E to W (1), or further restricted by separations between E and W (1), or occurrence only in the E (4).

A total of 11 species are assessed as Least Concern (LC) because they are widespread or well protected in reserves containing elephants. The remaining five species are assessed as Data Deficient (DD) because they are ecologically poorly known and are represented from few localities. These species include the only endemic southern African monogastric dung specialist (*C. bradshawi* van Lansberge, 1887), which could be facing threats.This discussion of wider distribution and conservation status is based on the older nomenclature, which precedes the soon to be published revision of Takano.

Catharsius aegeus

Génier, 2017

No synonyms

Global: LC (see IUCN Red List – LC; cited as *C. pandion* Harold, 1877)

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'MOZ.: CABO DELGADO | Mareja (site 3), P.N. Quirimbas' [NE Mozambique, Quirimbas National Park].

Taxonomy: Accepted species; recently found to comprise an undescribed species after having been wrongly identified as *C. pandion* Harold, 1877, which is an E coastal endemic (see species account); sexually dimorphic (head and prothoracic disc), prominence of characters varies with body size.

Distribution: Southern African savanna: N South Africa, NE Namibia, NE Botswana, Zimbabwe, Zambia, Malawi, Mozambique; reports from Angola, Democratic Republic of the Congo, Tanzania, require validation.

Locality data (mean ± SD, range): Average altitude: 792 ± 410, 55–1 477 m; average annual rainfall: 631 ± 166, 260–1 136 mm; average annual temperature (max. + min. /2): 20.7 ± 1.9, 16.9–25.2°C (N=48).

Habitat: No quantitative assessment; in Botswana; sampled on deep sands in open shrubland (70); few DBRU collection records on sand (2), sandy loam (1) in forest (3) or open woodland (2).

Food types: In Botswana: only sampled from carrion (chicken livers) (70), not sampled to any dung type, pig, elephant, cattle, sheep (all 0) (cited as *C. pandion* Harold); on Gauteng bushveld: sampled only to rotting sheep offal (4) not to any dung type, pig, horse, cattle (all 0); carrion specialisation may account for the few DBRU collection records: mixed human/cattle dung bait (2), gut contents of slaughtered impala (1); also cited from rotting fish, dead millipedes and in two instances from banana.

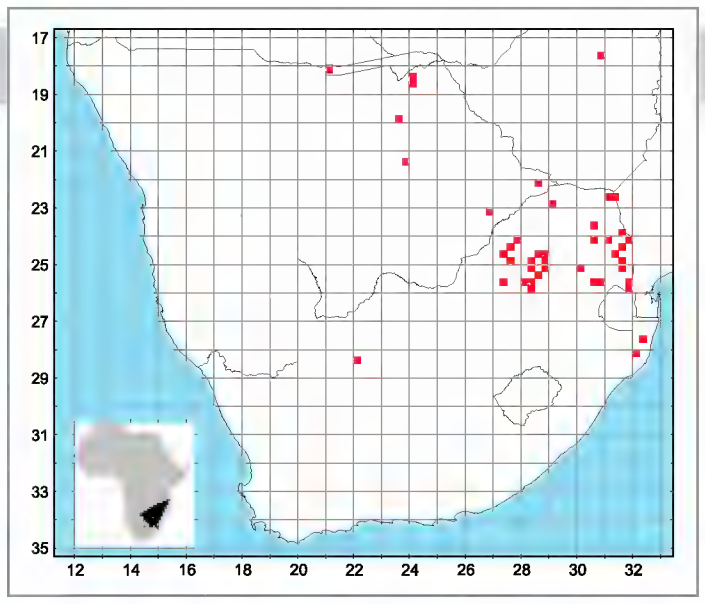
Temporal activity: Flight activity in darkness during the summer rainy season (Nov. to Jan.); attracted to light.

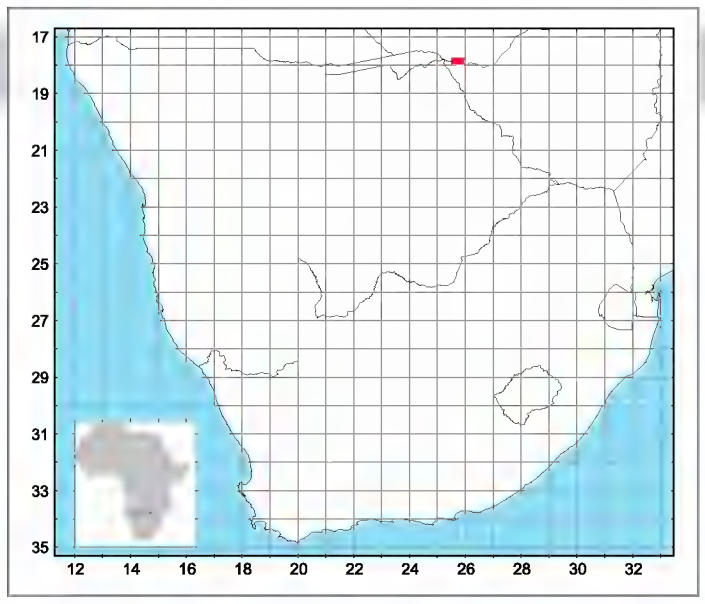
Ecoregions Namibia, Botswana, Zimbabwe: Zambezian and Mopane Woodlands (AT0725), Southern African Bushveld (AT0717); scattered records in Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian Baikiaea Woodlands (AT0726), Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Primarily in Central Bushveld (SVcb), Lowveld (SVl), Mopane (SVmp) (Savanna Biome).

Assessment rationale: EOO = 812 345 km^2 (underestimated); somewhat Data Deficient (DD), but probably a vegetation generalist and carrion specialist showing a bias to sandy soils, which would restrict the AOO; poor data from which to generate an assessment, but widespread records across farm rangeland and reserves suggest few threats at the present time; therefore, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on habitat associations and population density; protected in several national parks: Kruger (South Africa), Chobe (Botswana).





Catharsius bradshawi

van Lansberge, 1887

= *Catharsius insignis* Péringuey, 1892

Global: DD (see IUCN Red List – DD)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *C. bradshawi*: 'Afrique orient. : Zambèze' [presumably eastwards on the Zambezi River]; *C. insignis*: Not stated.

Taxonomy: Accepted species; sexually dimorphic (head and prothoracic disc), prominence of characters varies with body size.

Distribution: Difficult to assess owing to inexact localities for older reference specimens; recorded in the 1970s along the Zambezi River in N Zimbabwe; recorded in the 19th century along the Okavango and Evari rivers [Evari = upper reaches of Etaka River, NW of Etosha Pan] (DM, NCI) suggesting occurrence in N Botswana and N Namibia; also cited from Mozambique, which would, presumably, be an interpretation of the type locality.

Locality data (mean ± SD, range): Altitude: 717 ± 234, 373–895 m; annual rainfall: 650 ± 7, 641–659 mm; annual temperature (max. + min. /2): 23.6 ± 1.5, 22.4–25.9°C (N=4).

Habitat: No quantitative assessment; limited DBRU collection records on sandy loam (1), sandy clay loam (1) in grassland (2).

Food types: No quantitative assessment; limited DBRU collection records on dung of elephant (2), buffalo (1).

Temporal activity: Flight activity in darkness during the summer rainy season (Nov., Feb.).

Ecoregions Zimbabwe: Zambezian and Mopane Woodlands (AT0725) in the Zambezi Valley.

Assessment rationale: EOO = 52 950 km² (gross estimate, N Zimbabwe to upper Etaka River, N Namibia); not well represented in reference collections and poorly known ecologically; AOO probably much smaller than EOO due to possible bias to finer-grained soils in grassland on dung of monogastric herbivores, particularly elephant, but supporting quantitative data is required; rarity of modern reference material may be due to range contraction of monogastric herbivores, but this also requires testing; assessed as Data Deficient (DD), but may deserve an IUCN threat category.

Conservation measures: Before an assessment of conservation status may be made, a quantitative survey is required concentrating on reserves containing elephants on the floodplains along the Okavango and Zambezi river systems to determine the full EOO, AOO and ecological associations; protected in Victoria Falls National Park (Zimbabwe).

Catharsius calaharicus

Kolbe, 1893a

= *Catharsius disseptus* Péringuey, 1901 (but see Taxonomy)

Global: LC (See IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *C. calaharicus*: 'Kalahari-Wüste' [Kalahari Desert]; *C. disseptus*: 'Transvaal (Potchefstroom), Southern Rhodesia (between Limpopo and Zambesi Rivers)' [North-West Province, South Africa and W Zimbabwe].

Taxonomy: Accepted species; sexually dimorphic (head and prothoracic disc), prominence of characters varies with body size, removal of synonym pending.

Distribution: Deep Kalahari sands: Namibia, Botswana, E Zimbabwe, central N and NW South Africa.

Locality data (mean ± SD, range): Altitude: 1 062 ± 158, 581–1 689 m; annual rainfall: 329 ± 115, 157–659 mm; annual temperature (max. + min. /2): 19.9 ± 1.2, 17.7–23.0°C (N=152).

Habitat: No quantitative assessment; DBRU collection records primarily from deep sand (42), few from sandy loam (2); recorded in grassland (10), scrub/shrubland (17) and open woodland (14).

Food types: In Botswana: primarily sampled from omnivore: pig (84), and monogastric herbivore dung: elephant (62); few sampled from ruminant herbivore dung: sheep (5), cattle (0) or carrion (0); DBRU collection records from dung of elephant (3), donkey (4), horse (1), cattle (33), buffalo (1).

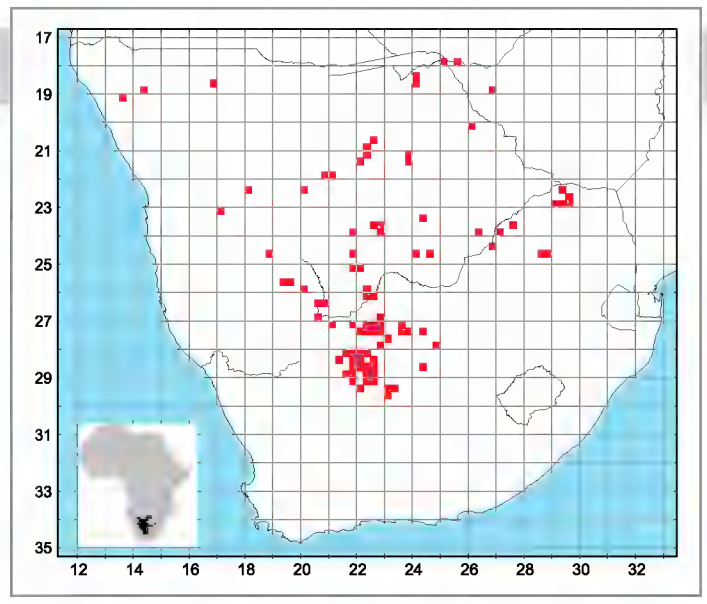
Temporal activity: Flight activity in darkness during the summer rainy season (Oct. to Apr.).

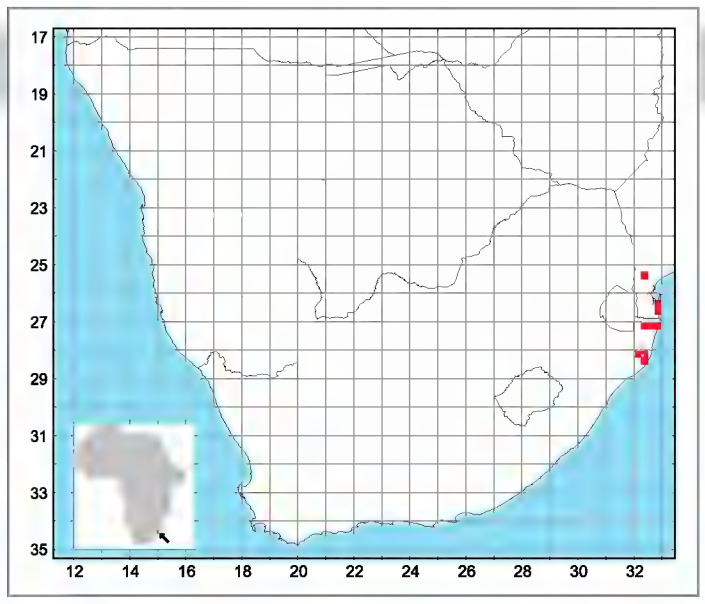
Ecoregions Namibia, Botswana, Zimbabwe: Centred on Kalahari Xeric Savanna (AT1309), Kalahari Acacia-Baikiaea Woodlands (AT0709).

Bioregions South Africa: Kalahari Duneveld (SVkd), East Kalahari Bushveld (SVk), NW Central Bushveld (SVcb), NW Mopane (SVmp) (Savanna Biome).

Assessment rationale: EOO = 639 850 km²; widespread, centred in an area used primarily for the grazing of domestic livestock from whose dung it has been widely recorded despite a quantitative bias to the dung of pig and elephant; transformation across its Northern Cape, South African range, only 0–2% (SVkd, SVk); assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on habitat associations and further data on food associations; widely represented in farm rangeland and protected in Chobe National Park, Central Kalahari Game Reserve and Kgalagadi Transfrontier Park (Botswana, South Africa).





Catharsius harpagus

Harold, 1877b (but see Taxonomy)

No synonyms

Global: DD

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'Afric. Austral' [southern Africa], lectotype: 'Delagoa Bay' [Maputo, S Mozambique].

Taxonomy: Accepted species, but name change pending; sexually dimorphic (head and prothoracic disc), prominence of characters varies with body size.

Distribution: Deep coastal sands of Maputaland Centre of Endemism; NE KwaZulu-Natal, South Africa; SE Mozambique.

Locality data (mean ± SD, range): Altitude: 28 ± 36, 0–117 m; annual rainfall: 801 ± 103, 661–971 mm; annual temperature (max. + min. /2): 22.2 ± 0.6, 21.3–23.6°C (N=12).

Habitat: No quantitative assessment of soil type; only two DBRU collection records on sand, but certainly a sand specialist; on sand in Maputo Special Reserve: restricted to grassland (192), forest (0).

Food types: No quantitative assessment; DBRU collection records on cattle dung (2); sampled in large numbers to pig dung.

Temporal activity: Flight activity in darkness, primarily in the summer rainy season (Oct. to May).

Ecoregions Mozambique: Maputaland Coastal Forest Mosaic (AT1119).

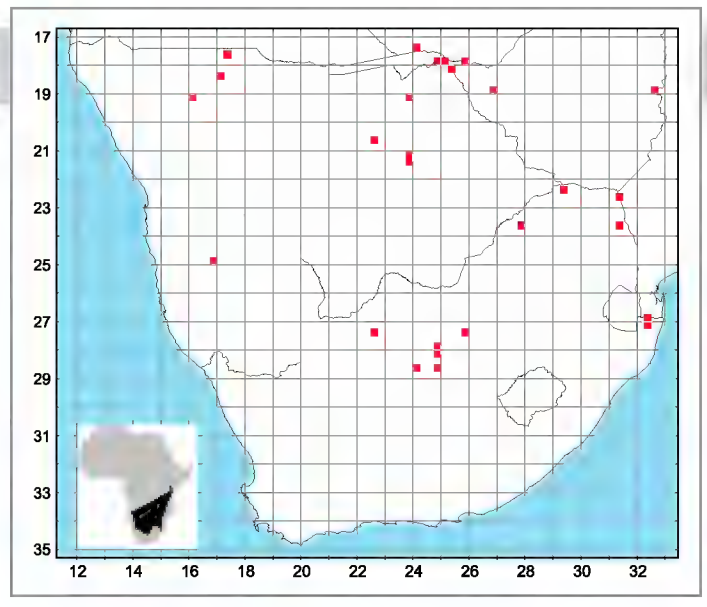
Bioregions South Africa: N Indian Ocean Coastal Belt Biome (CB); also margins of Lowveld (SVl) in adjoining Savanna Biome.

Assessment rationale: EOO = 8 250 km^2; difficult to assess conservation status in the absence of survey data to the N along the Mozambique coast or the absence of clear quantitative support for soil specialisation on coastal sands; assessed as Data Deficient (DD) although could equally deserve Least Concern (LC) status as part of the range is protected; may even deserve a threat category as the known EOO is < 20 000 km^2 and the AOO could be < 5 000 km^2; apparently centred on grassland patches within a forest/woodland matrix.

Conservation measures: Assessment of conservation status would be improved by a survey to determine soil and food associations, the number of occupied grassland patches, and population density; protected in Tembe Elephant Park and in iSimangaliso Wetland Park (World Heritage Site) (South Africa) plus Maputo Special Reserve (Mozambique) where there are a number of natural grassland patches on fossil lagoons.

Catharsius heros

Boheman, 1860



No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'juxta lacum N'Gami' [near Lake Ngami, N. Botswana].

Taxonomy: Accepted species; sexually dimorphic (head and prothoracic disc), prominence of characters varies with body size.

Distribution: Dry savanna from S to E Africa: South Africa, Namibia, Botswana, Zimbabwe, Angola, Mozambique, Kenya; occurrence now patchy due to dung type specialisation; most records outside of reserves older than 50 yr.

Locality data (mean ± SD, range): Altitude: 895 ± 368, 43–1 377 m; annual rainfall: 538 ± 169, 155–1 016 mm; annual temperature (max. + min. /2): 21.3 ± 2.0, 17.1–23.2°C (N=32).

Habitat: No quantitative assessment; most DBRU collection records from game reserves (15) or nearby localities (2); one record from a stray donkey holding pen (Kuruman); sandy soil, woody vegetation bias: sand (2), sandy loam (7), sandy clay loam (1) in open woodland (7), grassland (2).

Food types: In Botswana: bias to monogastric herbivore dung compared to other bait types: carrion (0), pig (2), elephant (18), cattle (0), sheep (0); all DBRU collection records from dung of large monogastric herbivores now found primarily in game reserves: elephant (12), rhinoceros (1), donkey (1).

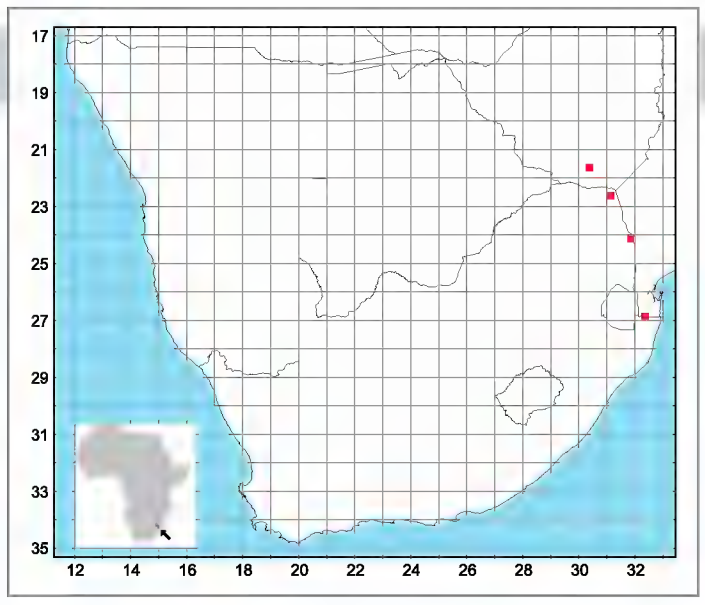
Temporal activity: Flight activity in darkness during the summer rainy season (Oct. to Apr.); attracted to light.

Ecoregions Namibia, Botswana, Zimbabwe: Namibian Savanna Woodlands (AT1316), Zambezian and Mopane Woodlands (AT0725), Angolan Mopane Woodlands (AT0702), Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian Baikiaea Woodlands (AT0726).

Bioregions South Africa: East Kalahari Bushveld (SVk), Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 3 687 200 km^2; AOO now much smaller, largely equivalent to the area of game reserves in dry savanna containing elephants and rhinoceros between southern and East Africa; one small-bodied individual recorded on donkey dung near Kuruman indicates that *C. heros* may also be present in very low population density where equids occur outside of reserves; currently assessed as Least Concern (LC) owing to protection in various reserves over a wide range.

Conservation measures: Conservation status largely dependent on continuing protection of elephants and rhinoceros in game reserves and national parks, including Kruger, Ndumu (South Africa), Chobe, Central Kalahari (Botswana), Etosha (Namibia), Bicuar (Angola), Hwange (Zimbabwe), Tsavo West (Kenya).



Catharsius laticeps

Boheman, 1857 (but see Taxonomy)

No synonyms

Global: DD

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'prope fluvium Limpopo' [close to Limpopo River, southern Africa].

Taxonomy: Subsequent to completion of this book, H. Takano (pers. comm.) pointed out that the true *C. laticeps* is a species of coastal forest on deep sands of NE KwaZulu-Natal and SE Mozambique (see Preamble) and is roughly sympatric with *C. pandion* Harold, 1877b; this wrongly-named species should be compared with *C. parafastidiosus* Ferreira, 1971, described from an unknown locality purported to be in South Africa; sexually dimorphic (head and prothoracic disc), prominence of characters varies with body size.

Distribution: Dry, warm, lowland savanna: S Zimbabwe, NE South Africa; also cited from Mozambique.

Locality data (mean ± SD, range): Altitude: 308 ± 209, 55–495 m; annual rainfall: 513 ± 96, 395–629 mm; annual temperature (max. + min. /2): 22.8 ± 0.2, 22.7–23.1°C (N=4).

Habitat: No quantitative assessment; one DBRU collection record on sandy clay loam in shrubland.

Food types: No quantitative assessment; limited DBRU collection records on the dung of elephant (1), cattle (1).

Temporal activity: Flight activity in darkness during the summer rainy season (Nov., Mar.).

Ecoregions Zimbabwe: margins of Zambezian and Mopane Woodlands (AT0725) and Southern African Bushveld (AT0717).

Bioregions South Africa: Mopane (SVmp), Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 15 750 km^2 (probably underestimated); not well represented in reference collections and poorly known ecologically; AOO possibly biased to finer-grained soils in open woody vegetation, but quantitative support required; insufficient data to determine if there is a bias to the dung of monogastric herbivores, which would influence conservation status; currently assessed as Data Deficient (DD).

Conservation measures: Before an assessment of conservation status can be made, a quantitative survey is required in drier savanna along the Limpopo River Valley and on the S Mozambique Coastal Plain to determine the full EOO, AOO and ecological associations; validation of the species name also required; protected in Kruger National Park and Ndumo Game Reserve (South Africa).

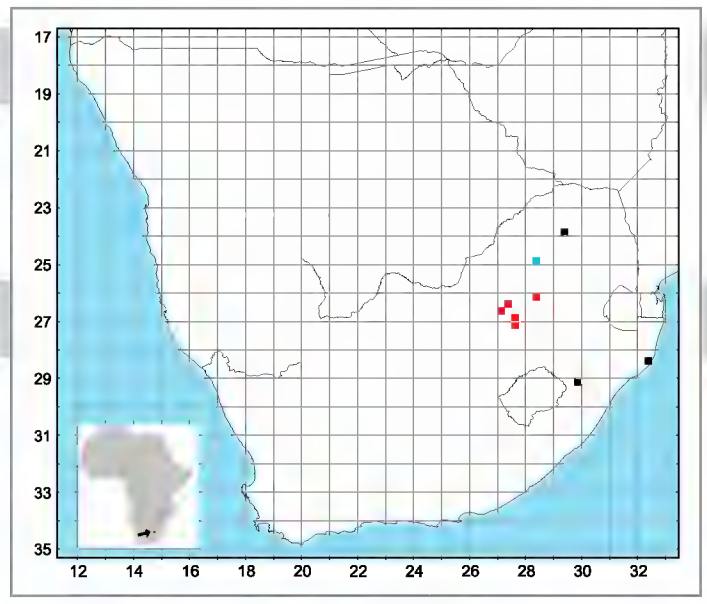
Catharsius longiceps

Gillet, 1907

= *Catharsius melancholicus sensu* Péringuey, 1901 (?*pars*)

Catharsius vansoni

Ferreira, 1960a (but see Taxonomy)



Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *C. longiceps*: 'Transvaal: Boksburg' [Boksburg, Gauteng, South Africa]; *C. melancholicus sensu* Péringuey: 'Natal (Estcourt, Durban), Transvaal (Boksburg, Lydenburg). Southern Rhodesia (Buluwayo, Salisbury)' [South Africa/Zimbabwe range possibly represents more than a single species]; *C. vansoni*: 'Transvaal: Potchefstroom' [Potchefstroom. North West Province, South Africa].

Taxonomy: Both *C. longiceps* and *C. vansoni* are, currently, accepted species; synonymy of *C. vansoni* pending publication; sexually dimorphic (head and prothoracic disc), prominence of characters varies with body size.

Distribution: Uncertain; recent samples localised near two type localities on NW Highveld, South Africa: Boksburg (*C. longiceps*) (blue square), Potchefstroom (*C. vansoni*) (red squares); old *C. vansoni* reference material from both non-validated Highveld and coastal localities (black squares); no material seen from Zimbabwe.

Locality data (mean ± SD, range): Altitude: 1 470 ± 68, 1 356–1 615 m; annual rainfall: 657 ± 28, 619–714 mm; annual temperature (max. + min. /2): 16.8 ± 0.3, 16.4–17.3°C (N=10); only for localities represented by red squares.

Habitat: In Abe Bailey Nature Reserve: sampled from sandy loam primarily in grassland (50) compared to open woodland (2).

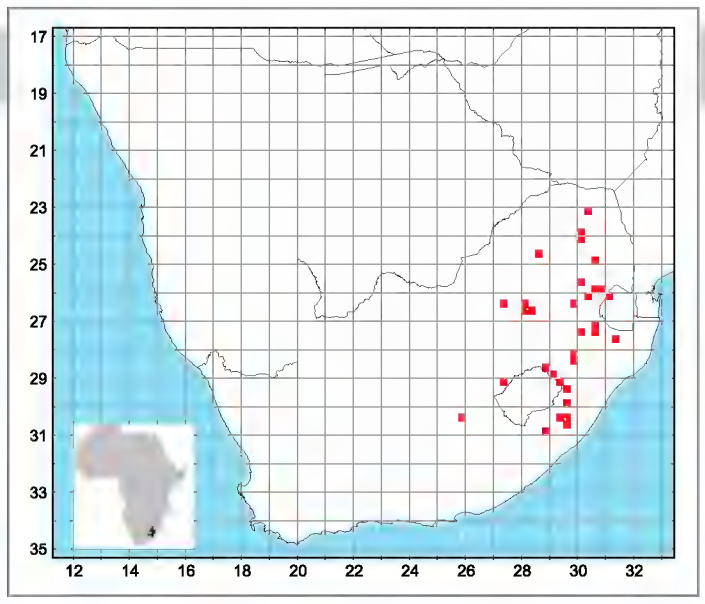
Food types: No quantitative assessment; sampled to cattle dung and composite baits of pig and cattle dung.

Temporal activity: Flight activity in darkness, primarily during the summer rainy season (Nov. to May).

Bioregions South Africa: Straddling NE and NW edges of Dry Highveld Grassland (Gh) and Mesic Highveld Grassland (Gm) (Grassland Biome) (red squares).

Assessment rationale: EOO = 6 130 km^2 (range for red squares only, presumably an underestimate); difficult to assess given the confused and meagre data; very small validated range in an area of North West Province where vegetation units are 25–50% transformed; however, presumably more widely distributed despite the absence of recent records elsewhere in southern Africa (previous 50 yrs); currently assessed as Data Deficient (DD).

Conservation measures: A survey is required to provide validated data on the EOO, AOO and ecological associations, and to generate a balanced assessment of conservation status; an assessment of the possible effects of habitat transformation would also be useful; currently known to be protected only in Abe Bailey Nature Reserve (South Africa).



Catharsius marcellus

Kolbe, 1893a

No synonyms

Global: LC
Endemic: RSA, Eswatini

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'In Zoutpansberg bei Mphôme in Nord-Transvaal' [Mphome Mission Station, Haenertsburg, Limpopo Province, South Africa].

Taxonomy: Accepted species; sexually dimorphic (head and prothoracic disc), prominence of characters varies with body size.

Distribution: Highveld Grassland: South Africa, Eswatini.

Locality data (mean ± SD, range): Altitude: 1 533 ± 383, 1 142–3 061 m; annual rainfall: 802 ± 127, 450–1 157 mm; annual temperature (max. + min. /2): 15.2 ± 2.3, 13.5–16.6°C (N=37).

Habitat: No quantitative assessment of soil type; DBRU collection records primarily from finer-grained soils: sandy clay loam (5), sandy loam (3), sand (1), all in pasture/grassland (8); bias to cooler grassland at Suikerbosrand Nature Reserve: montane grassland (31), Highveld Grassland (20), open woodland (5); at Carolina, little measured response to disturbance: natural *Themeda* grassland (44), fallow crop field (10), improved Kikuyu pasture (38).

Food types: No quantitative assessment; DBRU collection records entirely from cattle dung (10).

Temporal activity: Flight activity in darkness, primarily during the summer rainy season (Nov. to May).

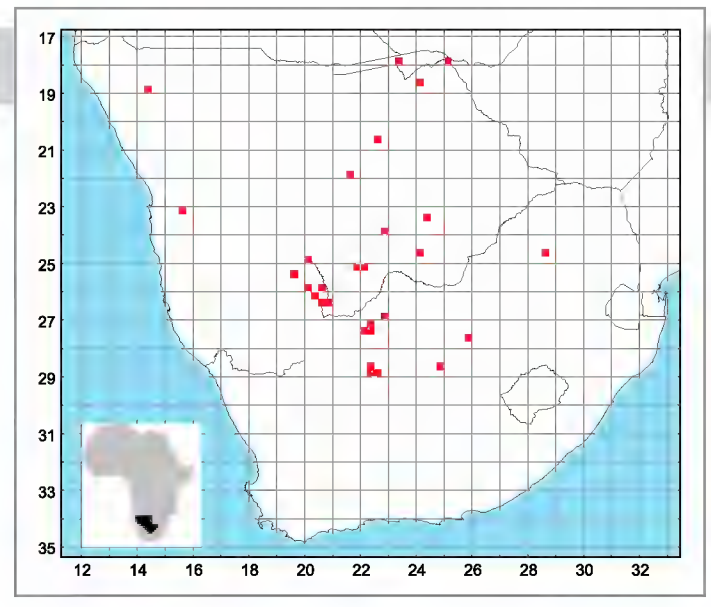
Bioregions South Africa: Centred on cooler moister vegetation units in the E Mesic Highveld Grassland (Gm), N Drakensberg Grassland (Gd) and N Sub-Escarpment Grassland (Gs); scattered records in W uplands of Gm and E Dry Highveld Grassland (Gh).

Assessment rationale: EOO = 126 300 km^2; widespread; readily attracted to cattle dung on the South African Highveld where it is still frequently recorded; available data suggest limited threats from pasture improvement and transformation, but most records appear to be from collections or quantitative studies conducted in natural grassland; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; in particular, the effects of pasture improvement and transformation should be reassessed to ensure that data from disturbed habitats at Carolina were not influenced by immigration from nearby natural grassland; protected in various reserves including Suikerbosrand, Ithala, Royal Natal, Lotheni.

Catharsius melancholicus

Boheman, 1860

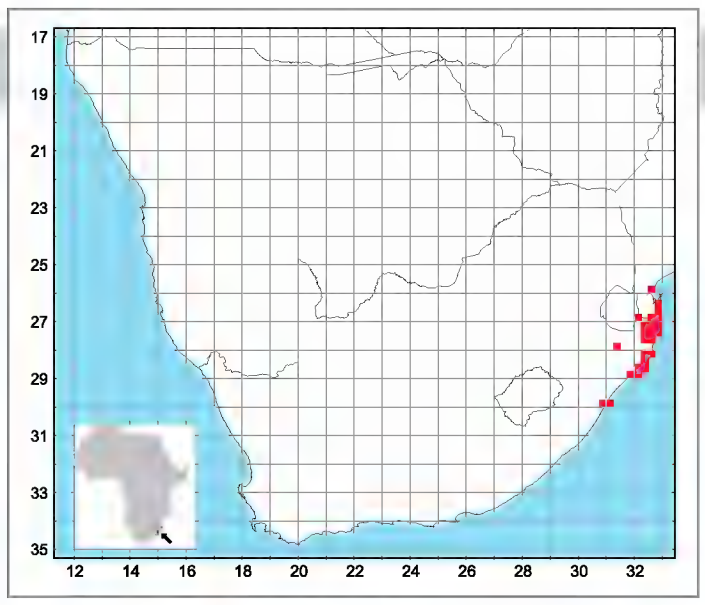


No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'prope lacum N'Gami' [close to Lake Ngami, N Botswana].
Taxonomy: Accepted species; sexually dimorphic (head, prothoracic disc), prominence of characters varies with body size.
Distribution: Deep sands of the Kalahari and its outliers: NW South Africa, Botswana, Namibia; also reported from Angola, Democratic Republic of the Congo (DRC); report from Mozambique presumably an error.
Locality data (mean ± SD, range): Altitude: 1 050 ± 108, 871–1 246 m; annual rainfall: 338 ± 137, 91–659 mm; annual temperature (max. + min. /2): 20.0 ± 1.3, 16.9–22.4°C (N=45).
Habitat: No quantitative assessment; sampled only from study sites on deep sand (29) in Botswana and Northern Cape, South Africa; DBRU collection records only on deep sand (3) in shrubland (3).
Food types: In Botswana: sampled mainly from carrion (chicken livers: 297), few on four dung types, pig (38), elephant (6), cattle (6), sheep (1); DBRU collection records only from a dead owl (1) and rotten goat meat (2).
Temporal activity: Flight activity during darkness in the summer rainy season (Dec. to Mar.).
Ecoregions Namibia, Botswana: Kalahari Xeric Savanna (AT1302), Namibian Savanna Woodlands (AT1316), Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian Baikiaea Woodlands (AT0726).
Bioregions South Africa: Kalahari Duneveld (SVkd), East Kalahari Bushveld (SVk) and sand outliers in Central Bushveld (SVcb) (Savanna Biome).
Assessment rationale: EOO = 970 820 km^2 (southern Africa only); SW half of EOO little transformed (0–2%, SVkd, E SVk) as land usage is dominated by grazing of domestic livestock; although, AOO would be about 30% smaller than EOO due to sand specialisation, food would be available for this carrion specialist throughout its range of which at least 10% is under protection; assessed as Least Concern (LC).
Conservation measures: Assessment of conservation status would be improved by quantitative data on habitat associations; protected in Chobe National Park, Central Kalahari Game Reserve and Kgalagadi Transfrontier Park (Botswana, South Africa).



Catharsius pandion

Harold, 1877b

= *Catharsius mossambicanus* Ferreira, 1960a

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'Port Natal' [Durban, KwaZulu-Natal, South Africa], lectotype: 'Natal' [KwaZulu-Natal, South Africa]; *C. mossambicanus*: 'Província de Moçambique: Lourenço Marques' [Maputo, Mozambique].

Taxonomy: Accepted species; *C. pandion* Harold was recently shown to be the senior name for *C. mossambicanus* Ferreira (Génier & Josso 2016) after having been assigned to a close, hitherto undescribed relative (now *C. aegeus* Génier, 2017); sexually dimorphic (head and prothoracic disc), prominence of characters varies with body size.

Distribution: Coastal range in KwaZulu-Natal, South Africa, and SE Mozambique, including the Maputaland Centre of Endemism.

Locality data (mean ± SD, range): Altitude: 43 ± 140, 0–991 m; annual rainfall: 853 ± 111, 646–1 010 mm; annual temperature (max. + min. /2): 21.9 ± 0.8, 17.7–23.3°C (N=52).

Habitat: In uMkhuze Game Reserve: entirely on sand (19), sandy clay loam and clay (0) (cited as *Catharsius* near *pandion*); on deep sand in Maputo Special Reserve, primarily in forest: coastal dune forest (15.8), inland sand forest patches (large: 13.8, medium: 9.9, small: 4.5), grassland (0.6); across a gradient of rehabilitating vegetation on coastal dunes at Richards Bay: grassland (68), dense early sucession woodland (1 135), open understorey later succession woodland (714), dense natural forest (1 072); largely supported by DBRU collection records: all on sand (8) in forest (15) or grassland (6).

Food types: No quantitative assessment; DBRU collection records from omnivore: human (4), monogastric: elephant (1) and ruminant herbivore dung: cattle (3).

Temporal activity: Flight activity in darkness, primarily during the summer rainy season (Oct. to Jan.), but also cooler dry season months on the warm coastline (Aug., May).

Ecoregions Mozambique: Maputaland Coastal Forest Mosaic (AT0119), Southern Zanzibar-Inhambane Coastal Forest Mosaic (AT0128).

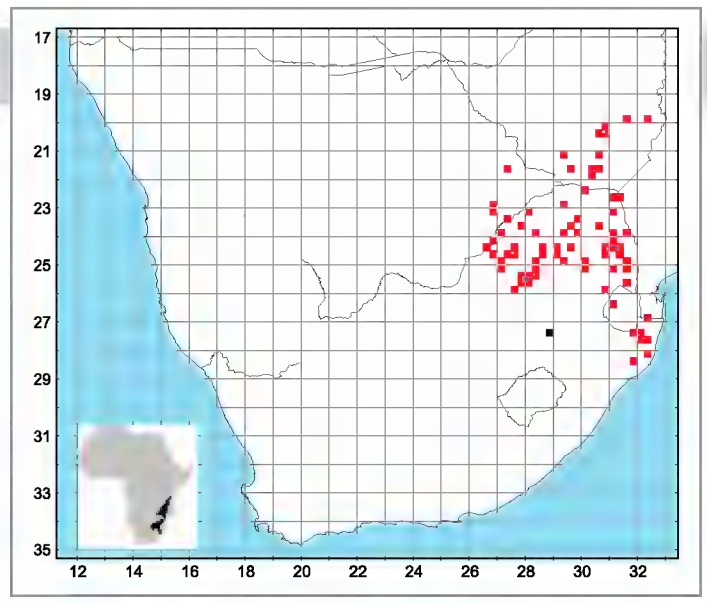
Bioregions South Africa: N Indian Ocean Coastal Belt Biome, adjoining edge of Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 18 650 km^2; occupies a limited coastal range where AOO is primarily restricted to Sand Forest (FOz 8) and Dune Forest; population density negatively influenced by small FOz 8 patch size; percentage transformation of FOz 8 unclear in South Africa, but listed as Critically Endangered due to clearance, firewood collection and elephant damage; Dune Forest threatened by mining of coastal dunes at S end of range although 30% of the concession is managed for post-mining vegetative restoration; protected across *ca.* 20% of known species range, therefore, currently assessed as Least Concern (LC) rather than Near Threatened (NT).

Conservation measures: Assessment of conservation status would be improved by quantitative data on food associations; as a forest specialist on range-restricted deep coastal sands, conservation status of this species is dependent on the continuing protection of large sand and dune forest patches in and around the Indian Ocean Coastal Belt; protected in iSimangaliso Wetland Park (World Heritage Site), Tembe Elephant Park (South Africa) and Maputo Special Reserve (Mozambique).

Catharsius philus

Kolbe, 1893a (but see Taxonomy)



No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'Senna in Mosambik…Sansibar.' [Mozambique: Sena; Tanzania: Zanzibar].

Taxonomy: Accepted species but name change and designation of a synonym pending; sexually dimorphic (head and prothoracic disc), prominence of characters varies with body size.

Distribution: Dry SE African savanna on finer-grained soils: N South Africa, E Botswana, SE and N Zimbabwe, Mozambique, E Tanzania; doubtful locality (black square).

Locality data (mean ± SD, range): Altitude: 783 ± 407, 48–1 850 m; annual rainfall: 617 ± 158, 326–1 136 mm; annual temperature (max. + min. /2): 20.5 ± 2.1, 13.4–25.7°C (N=94).

Habitat: On Gauteng bushveld: restricted to finer-grained soils: sandy clay loam (37), deep sand (0) with a bias to grassland (28) rather than open woodland (9) or shaded tickets (0); DBRU collection records indicate a bias to finer-grained soils: sandy clay loam (9), sandy loam (24), sand (8), and open woodland (25) as opposed to grassland/pasture (7) or even shrubland (5).

Food types: At Phalaborwa: sampling bias to dung of cattle (57) and pig (32), fewer on elephant (7); DBRU collection records primarily from ruminant herbivore dung: cattle (35), buffalo (1), wildebeest (2); few from monogastric herbivore dung: elephant (2), rhinoceros (1), horse (2).

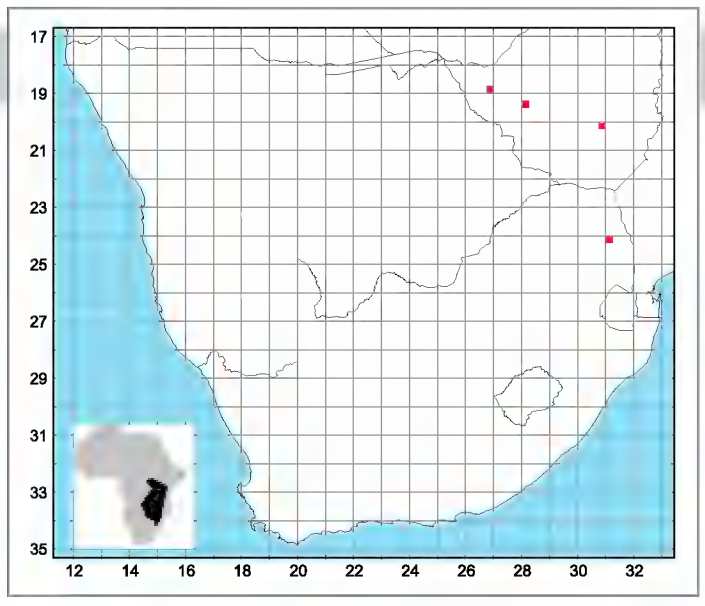
Temporal activity: Flight activity in darkness during the summer rainy season (Oct. to Apr.); on Gauteng bushveld: activity commences early summer (Oct., Nov.) peaks in mid-season (Dec., Jan.) and tails off in late summer (Feb. to Apr.); at Phalaborwa: much more abundant on a warm evening soon after very heavy rainfall (88) than on evenings following warm cloudy conditions and light rainfall (4) or hot, dry conditions (3).

Ecoregions Botswana, Zimbabwe: Southern African Bushveld (AT0717), S Zambezian and Mopane Woodlands (AT0725).

Bioregions South Africa: Central Bushveld (SVcb), Mopane (SVmp), Loweld (SVl) (Savanna Biome).

Assessment rationale: EOO = 774 500 km^2 (gross estimate); AOO probably smaller due to finer-grained soil bias in drier savanna; possible effect of woodland clearance difficult to assess owing to conflicting results; however, widespread occurrence on cattle dung in farm rangeland suggests few current threats; transformation in South African range, 0–58% (SVl), 2–49% (SVcb), 0–20% (SVmp); assessed as Least Concern (LC).

Conservation measures: Quantitative data on effects of woodland clearance on finer-grained soils would improve the assessment of conservation status; protected in Kruger National Park, Hluhluwe–iMfolozi Game Reserve, Tswaing Nature Reserve (South Africa).



Catharsius platycerus

(Klug, 1855) (but see Taxonomy)

= *Catharsius obtusicornis* Boheman, 1857
= *Catharsius gibbicollis* Gerstaecker, 1884
= *Catharsius princeps* Kolbe, 1893a

Global: DD

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Copris platycera*: 'Sena' [Mozambique]; *C. obtusicornis*: 'Caffraria interiore' [interior of SE South Africa]; *C. gibbicollis*: 'Massai' [East Africa]; *C. princeps*: 'Stanley Pool' [Democratic Republic of the Congo (DRC)].

Taxonomy: Accepted species, but change to validity of names and removal of some synonyms pending; sexually dimorphic (head and prothoracic disc), prominence of characters varies with body size.

Distribution: Dry to moist savanna from southern to East Africa, but very patchy occurrence due to dung type specialisation: South Africa, Zimbabwe, Mozambique, Democratic Republic of the Congo (DRC), Kenya; also reported from Namibia, Rwanda, Ethiopia.

Locality data (mean ± SD, range): Altitude: 568 ± 435, 59–1 106 m; annual rainfall: 704 ± 192, 529–1 136 mm; annual temperature (max. + min. /2): 23.2 ± 2.4, 19.8–25.9°C (N=8).

Habitat: No quantitative assessment; limited DBRU collection records (6) inconclusive: primarily from game reserves (5) on sand (1), sandy loam (1), sandy clay loam (2) in grassland (1), open woodland (3), forest (1).

Food types: No adequate quantitative assessment; at Phalaborwa: one specimen trapped to elephant rather than pig or cattle dung; limited DBRU collection records suggest bias to monogastric herbivore dung: rhinoceros (2), elephant (2), cattle (1).

Temporal activity: Flight activity in darkness during the summer rainy season (Nov. to Apr.); attracted to light.

Ecoregions Zimbabwe: Zambezian and Mopane Woodlands (AT0725), Zambezian Baikiaea Woodlands (AT0726), Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Mopane (SVmp) (Savanna Biome).

Assessment rationale: EOO = 3 012 810 km^2 (gross estimate); widespread, but rarely recorded; ecological data severely limited, but recent records primarily from game reserves of S and E Africa either on monogastric herbivore dung or attracted to light; does not qualify for threat status owing to large range and occurrence in many game reserves, but population density apparently very low; assessed as Data Deficient (DD).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations and population density; observations suggest that protection of elephant and rhinoceros in reserves is essential for the conservation of this species; protected in reserves from S to E Africa, including Meru, Masai Mara, Tsavo East (Kenya), Hwange (Zimbabwe), Gorongosa (Mozambique), Kruger (South Africa).

Catharsius sesostris

Waterhouse, 1888 (but see Taxonomy)

= *Copris pithecius* Olivier, 1790
= *Catharsius pylades* Péringuey, 1901

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *C. sesostris*: 'Egypt.'; *C. pithecius*: 'Sénégal' [Senegal; also reported from Egypt and East Indies by Olivier!]; *C. pylades*: 'Natal (Durban, Frere), Southern Rhodesia (Salisbury)' [KwaZulu-Natal, South Africa; Harare, Zimbabwe].

Taxonomy: Accepted species, but revalidation of one synonym and removal of all other species names pending; sexually dimorphic (head and prothoracic disc), prominence of characters varies with body size.

Distribution: Range reported to extend across West Africa (Senegal, Gambia, Cameroon), along E seaboard from South Africa to Egypt and into Middle East (Palestine, Syria, Jordan, Arabia); mapped taxon validated for NE South Africa, Zimbabwe, Zambia, Mozambique, Kenya; report from Namibia (Okahandja) requires validation.

Locality data (mean ± SD, range): Altitude: 993 ± 449, 1–1 958 m; annual rainfall: 757 ± 180, 383–1 415 mm; annual temperature (max. + min. /2): 19.3 ± 2.3, 14.3–25.9°C (N=96).

Habitat: On Gauteng bushveld: extreme sample bias to sand and strong bias to shaded situations, deep sand (48), sandy clay loam (0), grassland (1), open woodland (10), shaded thickets (37); DBRU collection records differ: sandy clay loam (5), sandy loam (10), sand (3) in grassland/pasture (9), shrub/woodland (3), forest (5).

Food types: On Gauteng bushveld: very strong sample bias to carrion (15) and omnivore dung pig (52), few on dung of horse (4), cattle (1); DBRU collection records differ: cattle (16), rhinoceros (3), horse (1), baboon (1), human/ruminant dung mixture (6).

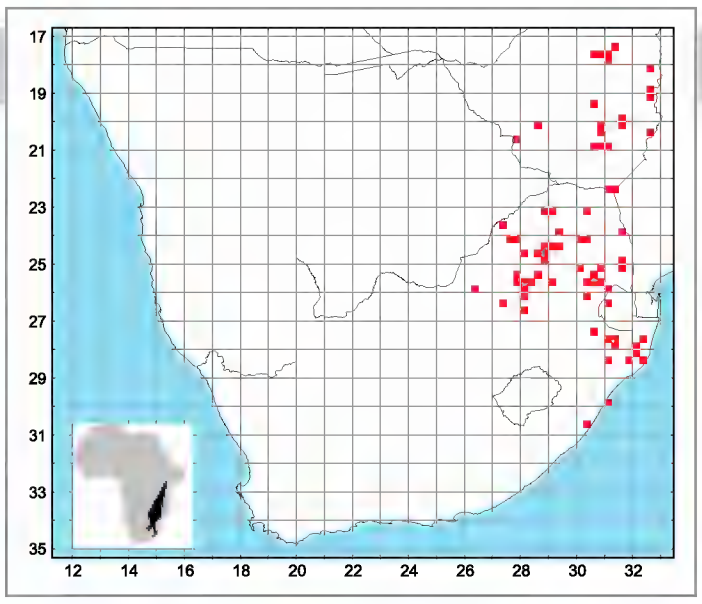
Temporal activity: Flight activity in darkness during the summer rainy season (Oct. to Apr.); on Gauteng bushveld activity spread evenly throughout summer.

Ecoregions Zimbabwe: Southern African Bushveld (AT0717), Southern Miombo Woodlands (AT0719); marginal in Zambezian and Mopane Woodlands (AT0725).

Bioregions South Africa: Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome); Indian Ocean Coastal Belt Biome (CB); marginal occurrence in Mopane (SVmp), E Mesic Highveld Grassland (Gm).

Assessment rationale: EOO = 5 293 770 km² (*C. sesostris* underestimated); EOO = 1 586 240 km² (mapped taxon); difficult to assess given questions of taxon identity, range and conflicting ecological data, but probably biased to omnivore dung in shady moist savanna, possibly on sandier soils; transformation in South Africa: 0–58% (SVl), 2–49% (SVcb), but not threatened at present due to widespread occurrence from S to E Africa and protection in many reserves; assessed as Least Concern (LC).

Conservation measures: Taxonomic issues concerning species identity need to be resolved; quantitative data suggest that protection of dense, moist, savanna woodland on sandy soils would be advantageous for the conservation of the taxon treated, here, as *C. sesostris*; protected in various reserves including, Kruger (South Africa), Lake Mutirikwe (Zimbabwe), Meru, Marsabit (Kenya).



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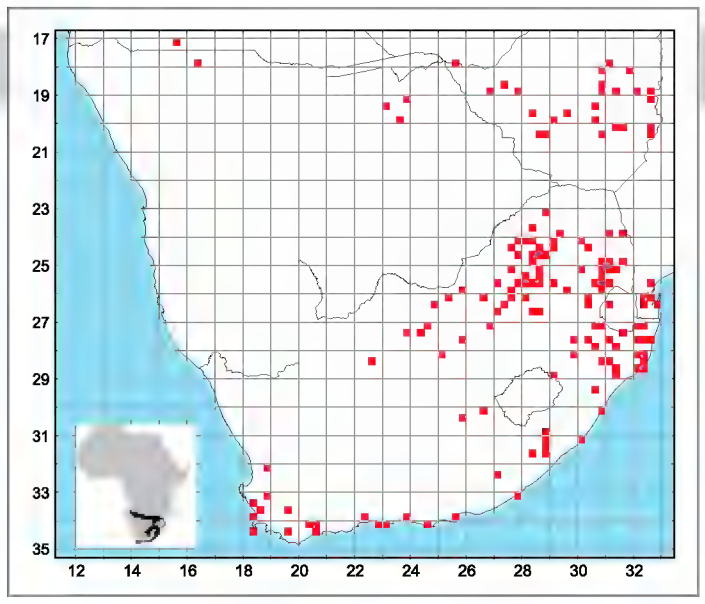

Catharsius tricornutus

(DeGeer, 1778)

= *Scarabaeus nemestrinus* Fabricius, 1781
= *Catharsius areolatus* Boheman, 1857
= *Catharsius dubius* Péringuey, 1901 (but see Taxonomy)

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Scarabaeus tricornutus*: Not stated; *S. nemestrinus*: 'Cap bon sp.' [Cape of Good Hope, South Africa]; *C. areolatus*: 'juxta fluvium Gariep' [near Orange River, South Africa]; *C. dubius*: 'Transvaal (Rustenburg), Southern Rhodesia (Zambesi River), Ovampoland (Okovango River)' [South Africa, Zimbabwe, Namibia].

Taxonomy: Accepted species; sexually dimorphic (head and prothoracic disc), prominence of characters varies with body size; removal of one synonym pending.

Distribution: Moist savanna and grasslands of southern Africa: S coastal to NE South Africa, Zimbabwe, Mozambique, N Botswana, N Namibia, S Angola; reports from Democratic Republic of the Congo (DRC), Zambia, Tanzania and Kenya require validation.

Locality data (mean ± SD, range): Altitude: 873 ± 549, 0–1 958 m; annual rainfall: 701 ± 204, 201–1 415 mm; annual temperature (max. + min. /2): 18.9 ± 2.4, 13.1–24.8°C (N=205).

Habitat: On Gauteng bushveld: extreme association with deep sand, but relatively generalist vegetation associations, deep sand (778), sandy clay loam (1), grassland (246), open woodland (353), shaded thickets (180); similar soil association in uMkhuze Game Reserve: sand (31), sandy clay loam/clay (0); partly supported by DBRU collection records: coarse-grained soil bias, but vegetation bias to grassland, clay (3), sandy clay loam (13), sandy loam (33), sand (43) in grassland/pasture (55), shrubland (8), open woodland (17); also crop fields (7).

Food types: On Gauteng bushveld: bias to dung of omnivores compared to monogastric and ruminant herbivores: pig (60), horse (24), cattle (13); but DBRU collection records primarily on cattle dung (96); also buffalo (1), elephant (4), horse (2), zebra (1).

Temporal activity: Flight activity in darkness during the summer rainy season (Oct. to May); on Gauteng bushveld: seasonal peak in early summer (Oct. to Jan.), tailing off to late summer (Feb. to Apr.); in mid-summer, flight activity peak at dusk (18:00–20:00) declining thereafter, but may fly sporadically throughout the night, particularly after showers; most Western and Eastern Cape records (11 out of 15) in spring (Oct.) or autumn (Mar. to May); attracted to light.

Ecoregions Namibia, Botswana, Zimbabwe, Mozambique: Maputaland Coastal Forest Mosaic (AT0119), Southern Zanzibar-Inhambane Coastal Forest Mosaic (AT0128), Southern African Bushveld (AT0717), Southern Miombo Woodlands (AT0719), Zambezian Baikiaea Woodlands (AT0726); Angolan Mopane Woodlands (AT0702).

Bioregions South Africa: East Kalahari Bushveld (SVk), Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome); moister, warmer, N and E Grassveld Biome: N Dry Highveld Grassland (Gh), E Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs); also Indian Ocean Coastal Belt, Albany Thicket and Fynbos Biomes.

Assessment rationale: EOO = 1 064 120 km² (possibly underestimated); AOO smaller due to soil type bias; nevertheless widespread in open vegetation and readily attracted to cattle dung in moist farm rangeland despite a bias to omnivore dung association; apparently adaptable to habitat disturbance as all 11 collection records in the Western and Eastern Cape were either in fallow crop fields (4) or grassland (7), suggesting range expansion from the summer rainfall region in response to clearance of natural shrubland; assessed as Least Concern (LC).

Conservation measures: None required owing to adaptability across a widespread range in farmland as well as reserves; protected in Hluhluwe–iMfolozi Game Reserve and various nature reserves, including Tswaing, Leeuwfontein, Roodeplaat (South Africa).

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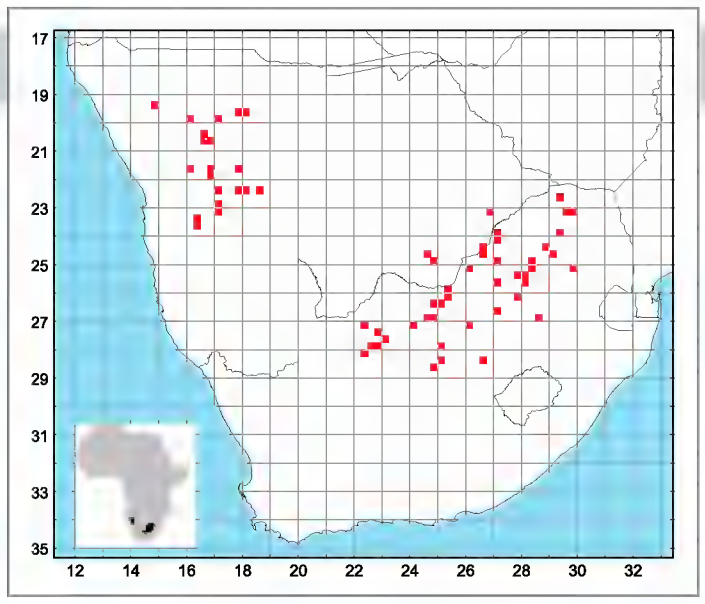


Catharsius ulysses

Boheman, 1857

No synonyms

Global: LC
Endemic: RSA, Botswana, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Caffraria tota' [all SE South Africa – undoubtedly inexact usage of 'Caffraria'].

Taxonomy: Accepted species; sexually dimorphic (head and prothoracic disc), prominence of characters varies with body size.

Distribution: Disjunct; centred on dry upland savanna or grassland: NW Highveld, South Africa, SE Botswana; N Namibian Plateau; report from Uganda presumably an error.

Locality data (mean ± SD, range): Altitude: 1 307 ± 253, 757–1 928 m; annual rainfall: 454 ± 130, 179–738 mm; annual temperature (max. + min. /2): 18.9 ± 1.5, 15.8–21.8°C (N=70).

Habitat: No quantitative assessment; DBRU collection records suggest a bias to sandier soils in open woody vegetation; clay (2), sandy clay loam (4), sandy loam (10), sand (21) in grassland (7), open shrubland (11), open woodland (17).

Food types: No quantitative assessment; DBRU collection records primarily from ruminant herbivore dung: cattle (35); monogastric herbivore dung: donkey (1).

Temporal activity: Flight activity during darkness, primarily in the summer rainy season (Nov. to May); attracted to light.

Ecoregions Namibia, Botswana: NW & SE Kalahari Xeric Savanna (AT1302), margins of three peripheral ecoregions.

Bioregions South Africa: East Kalahari Bushveld (SVk), Central Bushveld (SVcb) (Savanna Biome), N Dry Highveld Grassland (Gh) (Grassland Biome).

Assessment rationale: EOO = 367 200 km^2; widespread; in South Africa: E extreme of range little transformed (0–2%, E SVk), remainder variously transformed (13–42%, W SVk; 10–63%, N Gd; 14–49%, upland SVcb); however, readily attracted to cattle dung in fairly open vegetation in farm rangeland of both South Africa and Namibia, although few records from nature reserves; somewhat Data Deficient (DD) but assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations and population density in nature reserves versus adjoining farm rangeland; only known to be protected in Rustenburg, Benfontein and Dronfield nature reserves (South Africa).

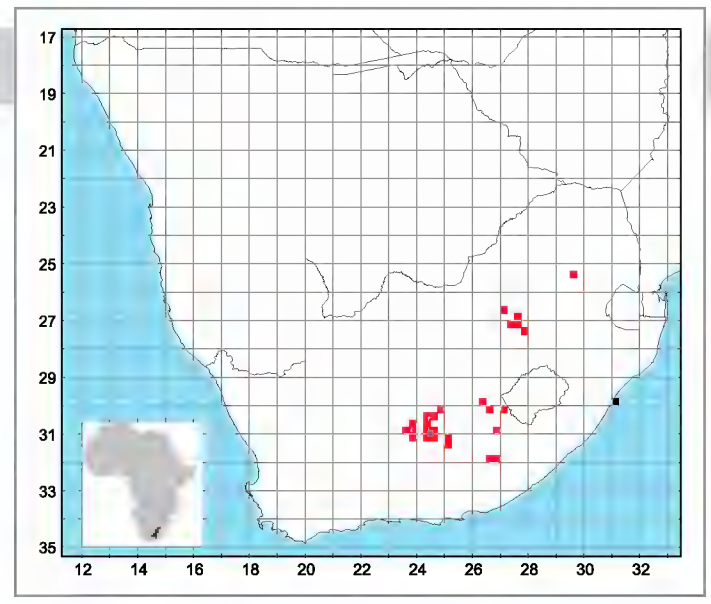
Catharsius vitulus

Boheman, 1857 (but see Taxonomy)

= *Catharsius camillus* Harold, 1877b

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: *C. vitulus*: 'Caffraria interiore' [interior of SE South Africa]; *C. camillus*: 'Port Natal' [Durban, South Africa, but probably a locality error], lectotype: 'cap b. sp.' [Cape of Good Hope, South Africa].

Taxonomy: Accepted species, but changes to validity of name and synonym pending; sexually dimorphic (head and prothoracic disc), prominence of characters varies with body size.

Distribution: Dry to arid, W Highveld and Upper Karoo, South Africa; Zimbabwe record requires validation; those from Democratic Republic of the Congo, Kenya and E coast of South Africa (black square: *C. camillus*) presumably errors.

Locality data (mean ± SD, range): Altitude: 1 385 ± 103, 1 151–1 632 m; annual rainfall: 404 ± 139, 266–676 mm; annual temperature (max. + min. /2): 15.3 ± 1.0, 13.4–18.3°C (N=40). Durban (black square) not included: 0.6 m, 955 mm, 20.8°C.

Habitat: No quantitative assessment; Upper Karoo samples from sand (14) or sandy loam (11) in grassland (14) or Karoo shrubland (13); limited DBRU collection records inconclusive: clay (1), sandy loam (3), sand (1) in pasture (3) and open woodland (1).

Food types: No quantitative assessment; DBRU collection records only from cattle dung (6).

Temporal activity: Flight activity in darkness during the summer rainy season (Nov. to May).

Bioregions South Africa: Primarily E Upper Karoo (NKu) (Nama Karoo Biome); Dry Highveld Grassland (Gh) (Grassland Biome); marginal records in Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs) (Grassland Biome).

Assessment rationale: EOO = 92 325 km² (minus Durban); patchy distribution possibly a collecting artefact, but may be related to some unidentified specialisation; SW part of range coincides with areas that have been little transformed; NE part of range 4–63% transformed (Gh); somewhat Data Deficient (DD), but assessed as Least Concern (LC) on basis of widespread range, 30% of which coincides with little modified regions in the Upper Karoo.

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations and the possible effects of modification of natural vegetation by pasture improvement; no available localities occurred in protected areas.

Genus *Copris* Geoffroy, 1762

Type species and designation: *Scarabaeus lunaris* Linnaeus, 1758, by subsequent designation (Latreille 1810).
Synonyms: None.
Last review: Selected Afrotropical groups revised by Nguyen-Phung and Cambefort (1986a, 1986b, 1987), Nguyen-Phung (1987, 1988a, 1988b, 1988c, 1989) and Cambefort (1992a, 1992b); phylogeny of entire Afrotropical *Copris* fauna (Cambefort & Nguyen-Phung 1996); partial reappraisal of *Copris* and allied genera (Marchisio & Zunino 2012); new species (Deschodt et al. 2015a).

The long-stablished genus, *Copris* Geoffroy, 1762, is widely distributed across climatically suitable areas. It is represented by a total of 346 species, some classified under subgeneric names that are variously considered to have generic status by some authors, or, to be invalid by others (*Copris* Geoffroy, 1762; *Paracopris* Balthasar, 1939a; *Microcopris* Balthasar, 1958; *Sinocopris* Ochi, Kon & Bai, 2009). *Copris* species have been recorded from the Afrotropical (108), Palaearctic (13), Oriental (99), Palaearctic + Oriental (1) and Nearctic (19) regions as well as the extreme NW of the Neotropical region (16).

The Afrotropical members of the genus have been divided into 48 species groups with 24 represented in the area encompassing South Africa, Botswana and Namibia. A total of 33 currently valid species is found in one or more of these three countries, although one is probably a synonym (see *Copris misellus* Péringuey under *C. obesus* Boheman). Another is represented by Kalahari and E coast subspecies. At least one undescribed species is also known.

Copris species are relatively large bodied although different groups show trends to either larger or smaller body size. Dung is buried at the ends of tunnels leading from under droppings. A number of species have been recorded to first sequester dung at the end of a shallow tunnels and then remove it to a deeper tunnel where separate brood ovoids are cut from a dung cake within a chamber. This nest architecture requires fairly large amounts of dung. Therefore, they are found primarily in moister regions that support large herbivores dropping large amounts of dung.

Copris species are mostly macropterous, flying during darkness, although a few species from cooler highland or southern regions may be diurnal fliers (Groups 17–18) or even apterous and flightless (Group 16). Of 32 valid species in southern Africa, 26 are restricted to the region with only six showing larger, more widespread ranges into the tropics.

Owing to patterns of relationships, it has been suggested that the history of the genus in Africa is concentrated on savanna with occasional local radiations into mountains and forest. However, in southern Africa, less than half of the species show ranges centred on northern savanna, either in the east (8), the west (3) or both (1). Others are centred on the Kalahari sands (2 + a subsp.) or across Highveld Grassland (3), possibly with a bias to the N (1) or the E escarpment (3). A number are southern endemics in the winter and bimodal regions, either along the W coast (1), S coast (4) or both (1). Others occur along the summer rainfall E coastal zone of South Africa (1), in Maputaland (1 + a subsp.), or northwards and up the Zambezi Valley (1). One shows a composite range along the S and E coasts and E escarpment. None are found in SW Arid regions.

Most *Copris* species are assessed as Least Concern (LC), since they are widespread in farmland and reserves (23) or are currently well protected in reserves along with elephants (1), although relatively few species appear to be coarse or omnivore dung specialists. However, several are assessed as Data Deficient (DD: 5), Near Threatened (NT: 1) or even Endangered (EN: 2). These eight species are poorly known ecologically and seven have been recorded at few localities. The three threatened species are endemic to the southern Cape where there has been extreme transformation of the natural fynbos or Renosterveld shrubland at lower altitude.

The system of groups suggested by Cambefort and Nguyen-Phung (1996) is used here, as it covers the entire Afrotropical fauna and is based on a morphological phylogeny. The patterns seem to describe serial radiations in different groups, some representing radiation into the same regions. There seems to be a bias to occurrence on herbivore dung, both that of monogastrics and ruminants.

In southern Africa:

Groups 1–3: Three species with basal phylogenetic derivation; two with eastern savanna associations in southern Africa, one primarily found in shady forest situations along the southern and E coasts as well as the E escarpment of South Africa.

Group 4: One monogastric herbivore dung specialist, with basal phylogenetic derivation, distributed in savannas from southern to E Africa.

Group 11: One species centred on deep sands of the southern Kalahari.

Major clade, mostly larger-bodied, more terminally derived.

Group 12: One species with two subspecies; both centred on deep sands in the southern Kalahari or Maputaland (NE coast South Africa).

Group 16: Two diurnally active, apterous, flightless species from the southern coast of South Africa; both assessed as at least EN owing to rarity of records from a highly transformed region.

Groups 17–18: Four species centred on cool moist or dry areas of the Highveld (3 spp.) or the highlands bordering the S coast, South Africa (1 sp.); possibly all showing diurnal flight; three species assessed as DD.

Groups 19–20: Three species centred on upland savanna in N Namibia (1 sp.) or Highveld Grassland (1 sp.) and S coast (1 sp.), South Africa.

Groups 21–22: Two species with distributions centred on the winter or winter and bimodal rainfall regions of South Africa.

Group 23: One savanna species widespread to East Africa.

Group 26: Two species centred on Highveld Grassland of South Africa or savanna in SE Africa.

Major clade, mostly smaller-bodied, more terminally derived.

Groups 30–31: Three species centred on Highveld Grassland, South Africa (1 sp.), upland savanna, N Namibia (1 sp.) or N Highveld Grassland and eastern savanna to East Africa (1 sp.).

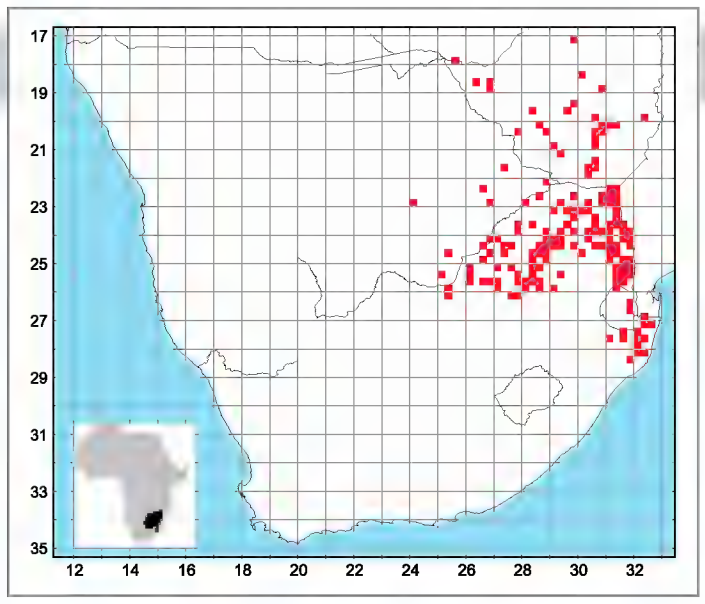
Group 38: One moist E coastal subspecies of a species found in moist savannas across tropical Africa.

Groups 39-40: Three species; two centred on dry savanna in N Namibia or in the east from South to East Africa; one with a distribution from the E coast up the Zambezi Valley.

Group 41: Two species centred on southern African savannas; one on coarse-grained soils in drier savanna; one on finer-grained soils in moister savanna.

Group 42: One species centred on SE African savanna.

Groups 47–48: Two species with distributions centred on deep sands of the southern Kalahari or Maputaland (NE coast South Africa).



Copris amyntor

Klug, 1855

= *Copris confusus* Boheman, 1857

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *C. amyntor*: 'Sena' [central Mozambique]; as *C. confusa*: 'Caffraria tota' [inexact, all SE South Africa].

Taxonomy: Accepted Group 42 species; sexually dimorphic (head, prothoracic disc), prominence of characters varies with body size.

Distribution: Widespread in drier, lower-altitude, eastern savanna woodlands from N South Africa across E Botswana, Zimbabwe Malawi and Mozambique; Kenyan records are undoubtedly confused with the closely related *C. harrisi* Waterhouse, 1891.

Locality data (mean ± SD, range): Altitude: 739 ± 421, 24–1 694 m; annual rainfall: 631 ± 149, 303–1 659 mm; annual temperature (max. + min. /2): 20.7 ± 1.9, 15.1–25.9°C (N=255).

Habitat: On Gauteng bushveld: restricted to finer-grained soils: sand (0), sandy clay loam (31), primarily in open woodland (24), grassland (3), shaded thickets (4); largely supported by uMkhuze Game Reserve data: sand (1), clay (11) and DBRU collection records: clay (7), sandy clay loam (25), sandy loam (42), sand (27) in shrub/woodland (73), pasture/grassland (16), crop fields (4).

Food types: At Phalaborwa: bias to dung of monogastric herbivores compared to ruminant herbivores and omnivores: elephant (26), cattle (3), pig (4); at SA Wildlife College: reduced population density where elephants are absent on finer-grained, gabbro-derived soils in farm rangeland, (1.7) compared to the Kruger National Park (33.0); DBRU collection records: elephant (35), rhinoceros (13), zebra (2); cattle (73), buffalo (9), wildebeest (2); baboon (1).

Temporal activity: Flight activity during darkness primarily in the early summer rainy season (Nov. to Jan.) tailing off into late summer (Feb. to Apr.) (Gauteng); in the warmer lowlands, recorded during the cool winter dry season (July) in elephant dung (Kruger National Park); attracted to light.

Ecoregions Botswana, Zimbabwe: Primarily Southern African Bushveld (AT0717), Zambezian and Mopane Woodlands (AT0725), Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Mainly Central Bushveld (SVcb), Mopane (SVmp) and Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 1 016 860 km^2; ecological data suggest that loss of elephants and clearance of woodland would impact on population density although collection data suggest that *C. amyntor* is sufficiently adaptable to remain extant over a wide area where transformation varies from 0 to 58% (SVl), 2–49% (SVcb), 0–20% (SVmp); assessed as Least Concern (LC).

Conservation measures: Quantitative data suggest that conservation status of *C. amyntor* will be enhanced by continued protection of elephants and woodland on finer-grained soils; protected in some lowland national parks: Kruger (South Africa), Gorongosa (Mozambique); also uMkhuze and Hluhluwe–iMfolozi game reserves (South Africa).

Copris anceus

(Olivier, 1789)

= *Copris minator* Harold, 1880

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Scarabaeus anceus*: Not stated. *C. minator*: 'Südafrika' [South Africa].

Taxonomy: Accepted Group 21 species; sexually dimorphic (head, prothoracic disc), prominence of characters varies with body size.

Distribution: Centred on the SW coast of South Africa (red squares) with tentative records from Namaqualand and S coastline (black squares); S coast record probably accurate.

Locality data (mean ± SD, range): Altitude: 77 ± 79, 0–340 m; annual rainfall: 270 ± 84, 95–475 mm; annual temperature (max. + min. /2): 16.7 ± 1.0, 14.8–18.5°C (N=35).

Habitat: No quantitative assessment of soil association, but DBRU collection records show a strong bias to deep coastal sands (18) compared to sandy loam (1); on deep sand in West Coast National Park: strong bias to natural shrubland (72) compared to adjacent sparse pasture (5) (now restored as shrubland); largely supported by DBRU collection records: scrub/shrubland (12), pasture/grassland (3), fallow crop fields (4).

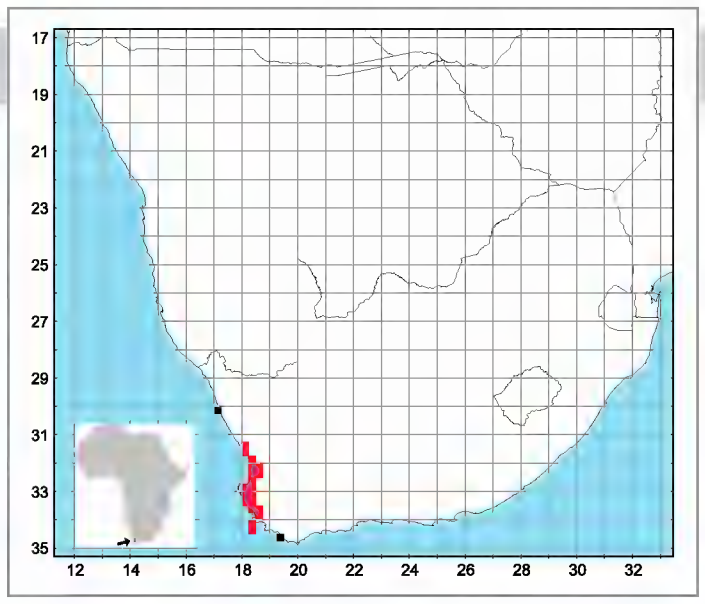
Food types: No quantitative assessment; DBRU collection records from cattle (17) and horse (1) dung.

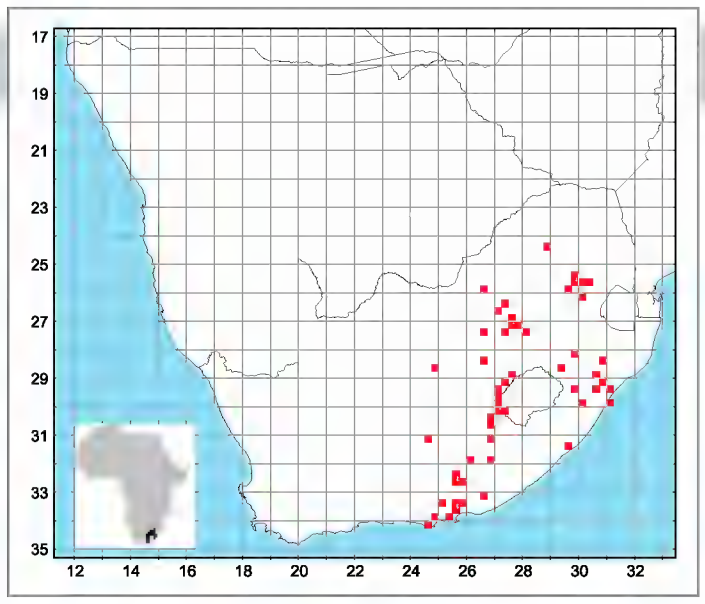
Temporal activity: Flight activity in darkness during warmer parts of the winter rainy season; on SW coast: primarily in spring (Aug., Sept.) tailing off into Oct. with few records in summer (Nov. to Mar.) and winter (June, July), but slightly more in autumn (Apr., May); evening flight varying in time with the onset of darkness.

Bioregions South Africa: Primarily centred on the W coastal extremes of the Fynbos Biome, particularly in vegetation units of the Western Strandveld (FS 1, 3, 5) and Sand Fynbos (FFd 3, 4, 5).

Assessment rationale: EOO = 7 625 km^2; although *C. anceus* has been recorded in fallow crop fields, clearance of natural vegetation drastically reduces population density; protected in several reserves although transformation due to urban development and cultivation varies from 25 to 80% across the main range (red squares); despite this small range centred on a highly transformed region, currently assessed as Least Concern, although monitoring of status would be useful.

Conservation measures: Assessment of conservation status would be improved by quantitative data on soil and food associations; protected in West Coast National Park, Cape of Good Hope Nature Reserve and the private Grotto Bay Nature Reserve.





Copris antares

Ferreira, 1958a

No synonyms

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Orange' [Free State, South Africa].
Taxonomy: Accepted Group 30 species; sexually dimorphic (head, prothoracic disc), prominence of characters varies with body size.
Distribution: Widespread at higher altitude on the Highveld and at lower altitude along the SE coast of South Africa.
Locality data (mean ± SD, range): Altitude: 1 136 ± 540, 1–1 860 m; annual rainfall: 628 ± 152, 327–961 mm; annual temperature (max. + min. /2): 16.5 ± 1.7, 13.0–20.8°C (N=61).
Habitat: No quantitative assessment; DBRU collection records from clay (1), sandy clay loam (8), sandy loam (14), sand (4) primarily in grassland/pasture (19), rarely in open woodland (1) and fallow crop fields (2).
Food types: No quantitative assessment; DBRU collection records from ruminant herbivore dung: cattle (33), buffalo (2), sheep (1).
Temporal activity: Flight activity in darkness, primarily during the summer rainy season (Oct. to May).
Bioregions South Africa: Centred on Dry Highveld Grassland (Gh), Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs) (Grassland Biome), and the lower-altitude Albany Thicket (AT) and Indian Ocean Coastal Belt (CB) biomes.
Assessment rationale: EOO = 269 985 km^2; widespread on the South African Highveld; no quantitative data available to support soil generalisation or determine if modification of natural grasslands would be detrimental to population density; extensive transformation due to cultivation occurs over much of its Grassland Biome range (2–50% Gh, 6–69% Gm, 2–40% Gs); currently assessed as Least Concern on basis of wide EOO.
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, particularly possible effects of natural grassland modification to improved pastures; nevertheless widespread in farmland; protected in Abe Bailey Nature Reserve and Addo Elephant National Park.

Copris bootes

Klug, 1855

= *Copris excavata* Klug, 1855
= *Copris bornemisszai* Ferreira, 1972

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *C. bootes*: 'Inhambane'; *C. excavata*: 'Inhambane' [SE Mozambique coast]; *C. bornemisszai*: 'Umfolozi (Natal)' [Hluhluwe–iMfolozi Game Reserve, KwaZulu-Natal, South Africa].

Taxonomy: Accepted Group 4 species; sexually dimorphic (head, prothoracic disc), prominence of characters varies with body size.

Distribution: Currently patchily distributed in moist, hot, lowland savannas from SE to E Africa: NE South Africa, N Botswana, Zimbabwe, Mozambique, Tanzania, Kenya; most available southern African records (19 out of 21) from game reserves or national parks.

Locality data (mean ± SD, range): Altitude: 497 ± 395, 0–1 106 m; annual rainfall: 740 ± 174, 511–1 136 mm; annual temperature (max. + min. /2): 22.4 ± 1.4, 20.5–25.9°C (N=19).

Habitat: No quantitative assessment: DBRU collection data from clay (1), sandy clay loam (2), sandy loam (8), deep sand (4), exclusively from wooded savanna: shrubland (2) or woodland (12).

Food types: In Botswana: sampled exclusively to elephant dung (17), none on dung of pig, cattle, sheep or on carrion (0); DBRU collection records dominated by monogastric herbivore dung: elephant (7), middens of hooked-lipped (black) or square-lipped (white) rhinoceros (10), horse (1), few on ruminant herbivore dung: buffalo (1), cattle (1).

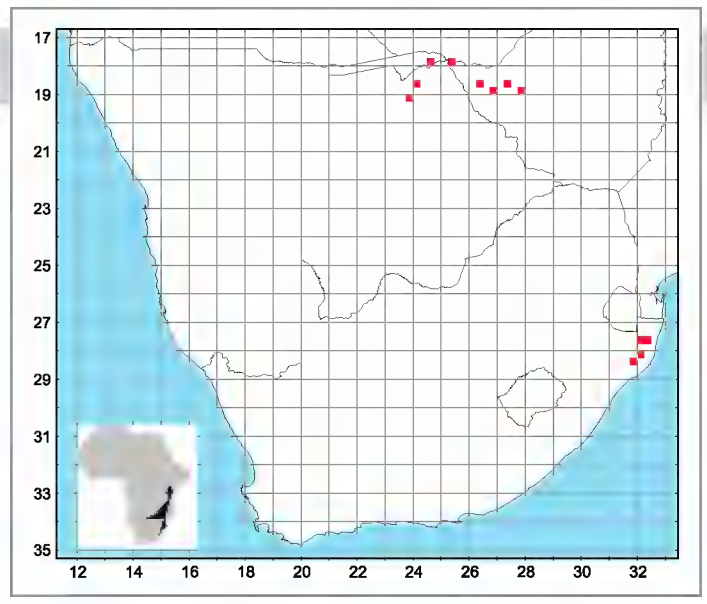
Temporal activity: Flight activity in darkness, primarily during the summer rainy season (Aug. to May).

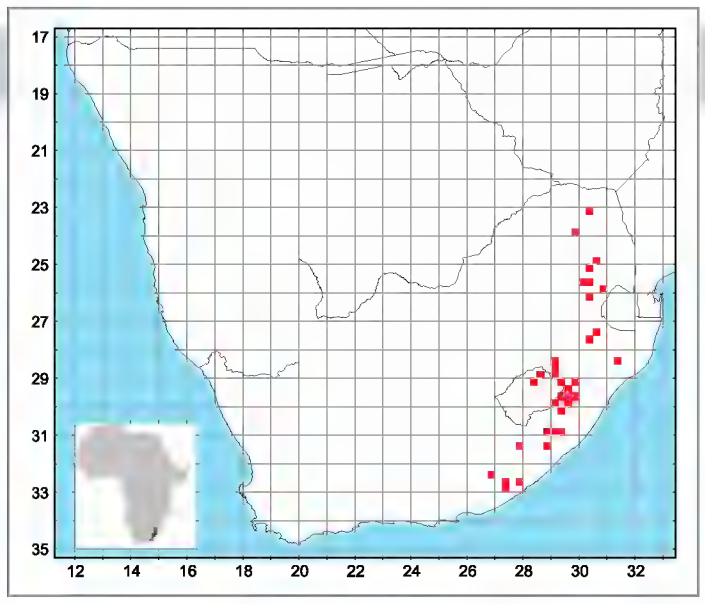
Ecoregions Botswana, Zimbabwe: Mostly in reserves bordering and within Zambezian Baikiaea Woodlands (AT1726).

Bioregions South Africa: Only in reserves in the south of the Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 959 800 km^2; AOO much smaller and almost exclusively restricted to game reserves in recent decades as reflected by patchy distribution; extreme association with elephant or rhinoceros dung, but protected over a very wide area in many reserves containing woodland; therefore, currently assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on habitat associations; dung and probable vegetation specialisation suggest conservation status is dependent on continuing protection of savanna woodlands and large monogastric herbivores in reserves; currently protected in various game reserves or national parks: uMkhuze, Hluhluwe–iMfolozi (South Africa), Hwange (Zimbabwe), Gorongosa (Mozambique), Chobe (Botswana), Manyara (Tanzania), Meru, Samburu, Amboseli (Kenya).





Copris caelatus

(Fabricius, 1794)

= *Copris contracta* Boheman, 1857

Global: LC
Endemic: RSA, Lesotho

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Scarabaeus caelatus*: 'Cap. Bon. Spei' [Cape of Good Hope, South Africa]; *C. contracta*: 'juxta fluvium Limpopo' [near Limpopo River, southern Africa].

Taxonomy: Accepted Group 17 species, but name requires validation; type(s) of *C. caelatus* need to be compared with those of S Cape species: *C. victorini* Boheman, *C. sexdentatus* Thunberg and *C. sphaeropterus* Harold; type locality of *C. contractus* (= *C. contracta*) inaccurate, but the species occurs nearby on the Soutpansberg; sexually dimorphic (head and prothoracic disc), prominence of characters varies with body size.

Distribution: Primarily moist to wet upper edges of E escarpment in both N (Limpopo, Mpumalanga, KwaZulu-Natal) and S (Eastern Cape); also descending to lower-altitude sub-escarpment levels in S; restricted to mid-summer rainfall region, South Africa.

Locality data (mean ± SD, range): Average altitude: 1 480 ± 473, 483–2 296 m; average annual rainfall: 792 ± 94, 626–1 047 mm; average annual temperature (max. + min. /2): 14.9 ± 2.5, 10.3–20.7°C (N=40).

Habitat: No quantitative assessment; DBRU collection records all from finer-grained soils: sandy loam (9), sandy clay loam (9) in pasture/grassland (17).

Food types: No quantitative assessment; DBRU collection records all from dung of cattle (22).

Temporal activity: Diurnal flight activity primarily in the summer rainy season (Sept. to May).

Bioregions South Africa: Primarily E edges of Mesic Highveld Grassland (Gm) and Drakensberg Grassland (Gd) plus lower-altitude Sub-Escarpment Grassland (Gs) (Grassland Biome).

Assessment rationale: EOO = 91 950 km^2; widespread along E escarpment, but no quantitative ecological data; however, habitat transformation low in areas showing greatest frequency of records along Lesotho and Eswatini borders; currently assessed as LC.

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, particularly data on effects of habitat transformation and pasture improvement; protected in the uKhahlamba Drakensberg Park (World Heritage Site) of the central Drakensberg.

Copris cambeforti

Nguyen-Phung, 1988a

No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Transvaal, P. N. Kruger' [Kruger National Park, South Africa].

Taxonomy: Accepted Group 2 species; sexually dimorphic (head, prothoracic disc), prominence of characters varies with body size.

Distribution: Known from only two spot localities in N South Africa; Blouberg (may be inexact) and Punda Milia area (Lowveld).

Locality data (mean ± SD, range): Altitude: 952 ± 694, 461–1 443 m; annual rainfall: 578 ± 77, 523–632 mm; annual temperature (max. + min. /2): 20.0 ± 4.0, 17.2–22.9°C (N=2).

Habitat: A single DBRU observation on sand in open woodland.

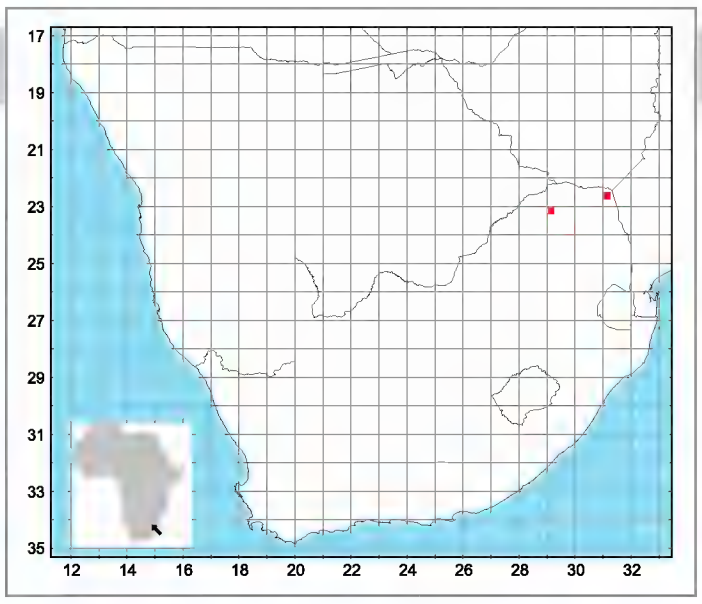
Food types: A single DBRU observation from elephant dung.

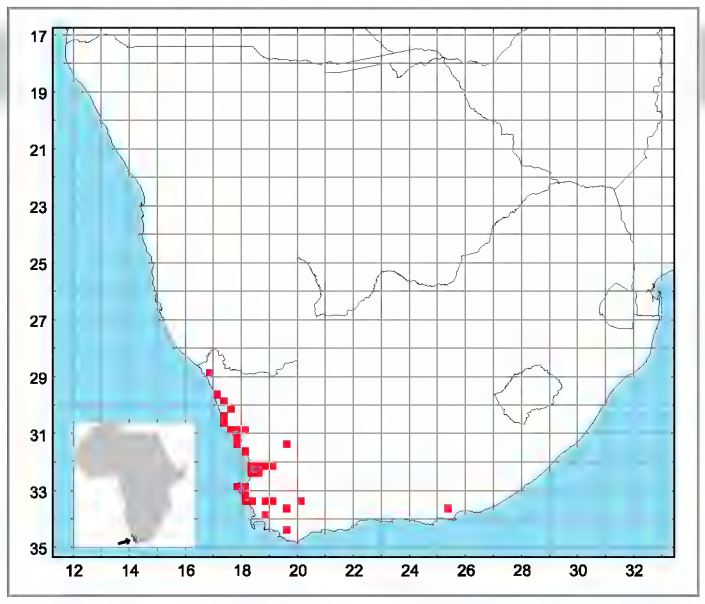
Temporal activity: Flight activity in darkness; recorded in the summer rainy season (Mar.).

Bioregions South Africa: Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 540 km² (underestimated); known from few, somewhat inexact localities, therefore, assessed as Data Deficient (DD).

Conservation measures: A survey is required to determine its full EOO, AOO and ecological associations before an assessment may be made of its conservation status; protected in the Kruger National Park.





Copris capensis

Waterhouse, 1891

No synonyms

Global: LC (see IUCN Red List – DD)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'South Africa'.
Taxonomy: Accepted Group 22 species; sexually dimorphic (head, prothoracic disc); prominence of characters varies with body size.
Distribution: Within the winter rainfall region of South Africa on the W coast and SW hinterland; also a single record from the Eastern Cape in the E of the bimodal rainfall region.
Locality data (mean ± SD, range): Altitude: 175 ± 213, 0–1 007 m; annual rainfall: 205 ± 95, 54–430 mm; annual temperature (max. + min. /2): 17.1 ± 1.1, 15.0–18.6°C (N=43).
Habitat: No quantitative assessment; DBRU collection records biased to coarse-grained soils: sand (17), sandy loam (6), sandy clay loam (1), with a possible bias to more open vegetation: scrub/shrubland (6), grassland/pasture replacing natural shrubland (10) and tolerance of disturbance: fallow crop fields (6).
Food types: No quantitative assessment; DBRU collection records primarily from cattle dung (22) with two from horse dung.
Temporal activity: Flight activity in darkness; primarily during the winter rainy season across its main W range (Apr. to Oct.).
Bioregions South Africa: In N: Centred on Namaqualand Sandveld (Sks) (Succulent Karoo Biome); In S: Scattered across vegetation units of Western Strandveld (FS), Sand Fynbos (FFd), Sandstone Fynbos (FFs), Granite Renosterveld (FRg) and Shale Renosterveld (FRs) (Fynbos Biome).
Assessment rationale: EOO = 45 395 km^2; apparently some tolerance to vegetation transformation (dry pastures, crop fields); possibly owing to high frequency occurrence in low profile, natural scrub and shrubland of arid areas; IUCN Red List as Data Deficient (DD) now re-assessed as Least Concern (LC) on basis of widespread occurrence in the mostly little-transformed vegetation of Namaqualand (3–10%); however, only recorded in low population density in the more extensively transformed S of its range (17–90%, higher on finer-grained soils).
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, particularly soil type associations and the effects on population density of clearance of natural scrub or shrubland; protected in two national parks: West Coast, coastal part of Namaqua.

Copris cassius

Péringuey, 1901

= *Copris cassius* Péringuey, 1901, subsp. *angolensis* Ferreira, 1962a

Global: LC
Endemic: RSA, Botswana, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *C. cassius*: 'British Bechuanaland (Kanye)' [Kanye, Botswana]. subsp. *angolensis*: 'Acampamento da Reserva de Caça da Cameia' [Angola: Cameia National Park, campsite].

Taxonomy: Accepted Group 47 species; sexually dimorphic (head, prothoracic disc), prominence of characters varies with body size; assuming that the bias in locality records to the SW Kalahari is not a collection artefact (see habitat notes); the synonymy of subsp. *angolensis* should be re-assessed.

Distribution: Centred on the SW Kalahari with occurrence in deep sand outliers at the eastern edge of the range.

Locality data (mean ± SD, range): Altitude: 1 161 ± 157, 839–1 512 m; annual rainfall: 372 ± 106, 191–689 mm; annual temperature (max. + min. /2): 19.2 ± 1.0, 15.7–21.3°C (N=92).

Habitat: On Gauteng bushveld: restricted to deep sands (179), sandy clay loam (0) and biased to open vegetation, grassland (172), open woodland (6), shaded thickets (1); on deep sands in Botswana: only in open vegetation (grassland, shrubland) of the arid SW (28) not moister, wooded NE (0); largely supported by DBRU collection records: sand (47), sandy loam (3), in grassland (22), shrubland (13) or open woodland (12).

Food types: In Botswana: poorly attracted to dung of ruminant herbivores (cattle: 2) or omnivores (pig: 2), instead biased to dung of monogastric herbivores, (elephant: 24) even though elephants are absent from the arid SW; absent from carrion (chicken livers) and sheep pellets (0); DBRU collection records primarily from dung of cattle (42), also horse/donkey (5).

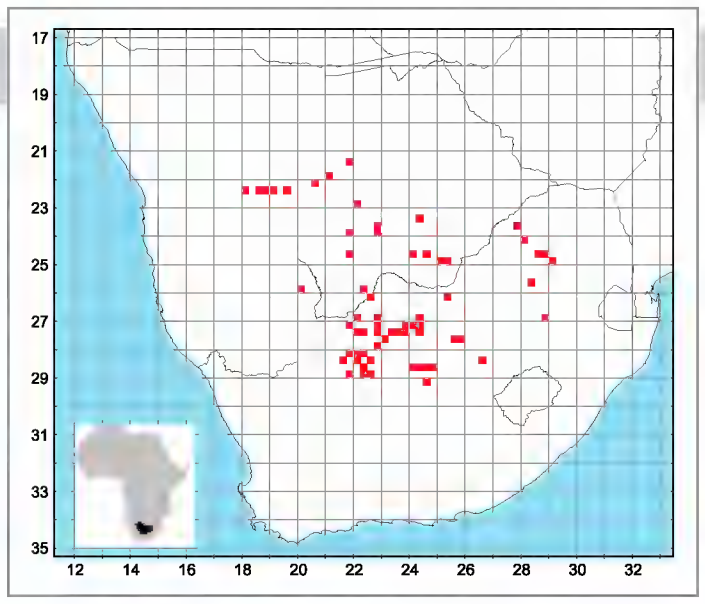
Temporal activity: Flight activity during darkness, primarily during the summer rainy season (Oct. to May); on Gauteng bushveld: primarily active in early summer (Oct. to Jan.) tailing off to late summer (Feb. to Apr.) and autumn (May).

Ecoregions Namibia, Botswana: Kalahari Xeric Savanna (AT1309).

Bioregions South Africa: Primarily centred on the Eastern Kalahari Bushveld Bioregion (SVk) with records in the Kalahari Duneveld (SVkd) and deep sand outliers of the Central Bushveld (SVcb) (Savanna Biome).

Assessment rationale: EOO = 547 290 km² (southern range); SW Kalahari range coincides with areas of deep sand used primarily for grazing of livestock; transformation (cultivation) limited although this increases to the east (2–25%, SVk; 4–24%, sandy units in SVcb); however, this may not be detrimental to population density owing to recorded association with grassland; assessed as Least Concern (LC).

Conservation measures: Owing to conflicting results, assessment of conservation status would be improved by further quantitative data on food associations; protected in Khutse Game Reserve (Botswana), Tswalu Kalahari Reserve and Nylsvlei Nature Reserve (South Africa).



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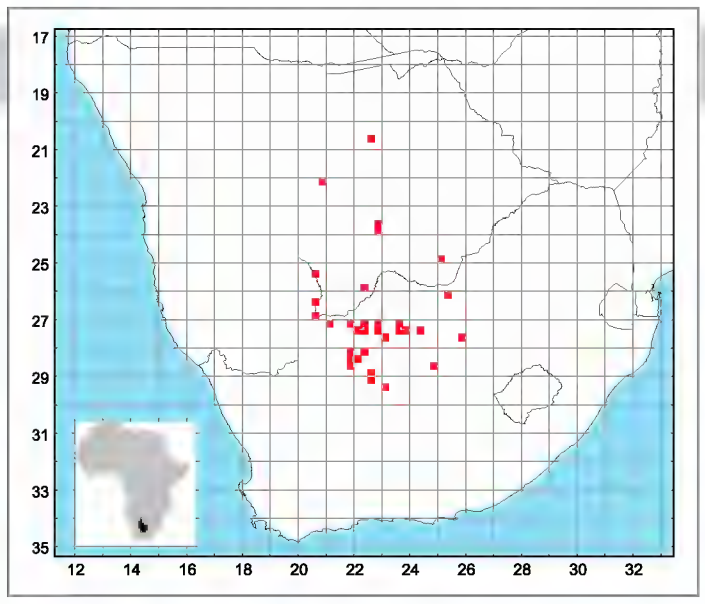


Copris cornifrons

Boheman, 1860

= *Copris curvicornis* Boheman, 1860
= *Copris achates* Péringuey, 1901

Global: LC
Endemic: RSA, Botswana

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *C. cornifrons*: 'juxta lacum N'Gami' [near Lake Ngami, Botswana]; *C. curvicornis*: 'juxta lacum N'Gami'; *C. achates*: '? N'Gami-land' [N Botswana].

Taxonomy: Accepted Group 11 species; sexually dimorphic (head, prothoracic disc), prominence of characters varies with body size.

Distribution: Restricted to the dry to arid southwest Kalahari.

Locality data (mean ± SD, range): Altitude: 1 111 ± 153, 830–1 367 m; annual rainfall: 312 ± 90, 157–491 mm; annual temperature (max. + min. /2): 19.4 ± 1.1, 17.5–22.4°C (N=38).

Habitat: No quantitative assessment; DBRU collection records almost exclusively from deep sand (20), sandy loam (1) in open vegetation: grassland (8), open shrubland (10), open woodland (3).

Food types: No quantitative assessment; DBRU collection records primarily from cattle dung (16), also horse/donkey dung (3).

Temporal activity: Flight activity in darkness, primarily during the summer rainy season (Sept. to Apr.).

Ecoregions Botswana: E Kalahari Xeric Savanna (AT1309).

Bioregions South Africa: Centred on the Kalahari Duneveld (SVkd) and Eastern Kalahari Bushveld (SVk) (Savanna Biome).

Assessment rationale: EOO = 286 300 km^2; EOO ~equivalent to widespread AOO across an area of deep sands used primarily for the grazing of farm livestock on whose dung it has been recorded in low population density; transformation 0–2% over most of RSA range (SVkd, W of SVk); assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, particularly further investigation to determine if population density is naturally low or an artefact of available data; a recent quantitative gradsect study from NE to SW across the Botswana Kalahari recorded only a single individual attracted to elephant dung bait; protected in Kgalagadi Transfrontier Park and Tswalu Kalahari Reserve (Botswana, South Africa).

Copris corniger

Sahlberg, 1823

= *Copris lunarioides* Waterhouse, 1891 (*pars*)
= *Copris laticornis* Péringuey, 1901 (*pars*)

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *C. cornigera*: Not stated; *C. lunarioides pars*: 'S. Africa' [South Africa]; *C. laticornis pars*: 'Cape Colony (Albany, Alexandria)' [Eastern Cape, South Africa].

Taxonomy: Accepted Group 26 sexually dimorphic (head, prothoracic disc), prominence of characters varies with body size.

Distribution: Highveld Grassland to the N and Eastern Cape lowlands to the SE; on a 500–2 800 m gradsect from coastal hills to Sani Pass, KwaZulu-Natal, recorded only at 1 000–1 500 m.

Locality data (mean ± SD, range): Altitude: 1 356 ± 429, 0–2 274 m; annual rainfall: 718 ± 127, 371–1 121 mm; annual temperature (max. + min. /2): 15.5 ± 1.7, 10.6–20.5°C (N=90).

Habitat: At Carolina: sampled from improved Kikuyu grass pasture (5) and fallow crop fields (1), but not natural *Themeda* grassland (0); DBRU collection records suggest a bias to finer-grained soils: clay (1), sandy clay loam (22), sandy loam (15), sand (1) mainly in pasture/grassland (33), rather than open shrub/woodland (3).

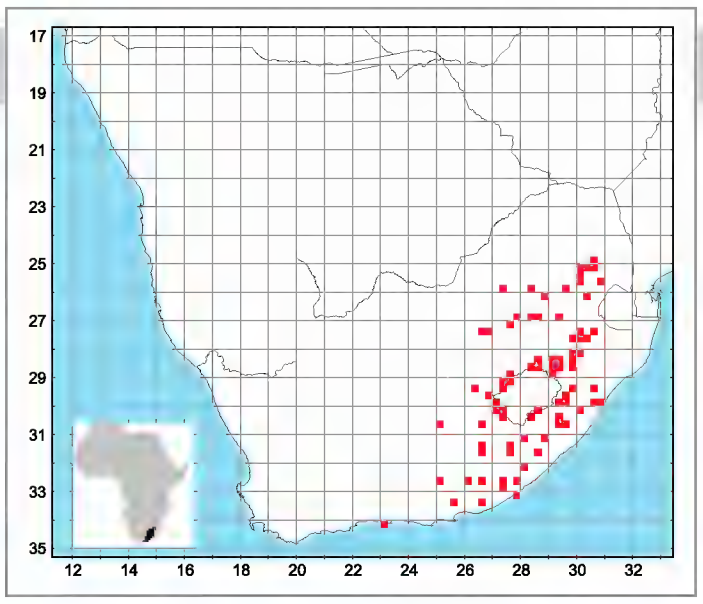
Food types: No quantitative assessment; DBRU collection records primarily from cattle dung (44), one from horse dung.

Temporal activity: Evening flight activity in darkness during the summer rainy season (Oct. to Apr.).

Bioregions South Africa: Centred on Dry Highveld Grassland (Gh), Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs) and margins of the Drakensberg Grassland (Gd) (Grassland Biome) with marginal occurrence in three coastal bioregions.

Assessment rationale: EOO = 318 935 km^2; widespread across the farmland on Highveld grasslands where it is readily attracted to the dung of domestic livestock, particularly that of cattle; data from Carolina may indicate that *C. corniger* is fairly adaptable to grassland modification, although extensive transformation due to cultivation occurs over much of the Grassland Biome (4–60% Gh, 6–69% Gm, 2–50% Gs); assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative ecological data; protected in Golden Gate National Park.



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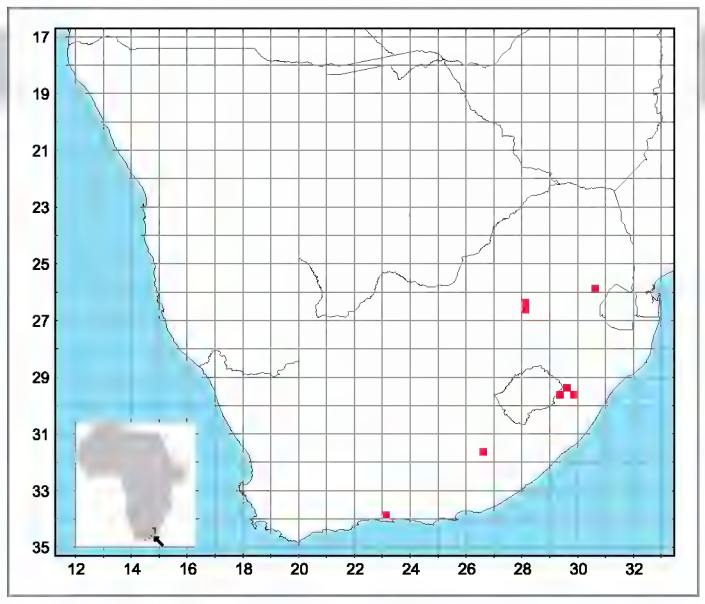


Copris crassus

Deschodt & Davis, 2015 (see Deschodt et al. 2015a)

No synonyms

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Suikerbosrand Nat. Res., Gauteng, South Africa, 28°28-32'S 28°10-17'E'.

Taxonomy: Accepted Group 3 species; sexually dimorphic (head, prothoracic disc), prominence of characters varies with body size.

Distribution: Moist South African highlands; N edge of Highveld and E escarpment edge from Mpumalanga and KwaZulu-Natal to the Eastern Cape; occurs at lower altitude at the S range limits.

Locality data (mean ± SD, range): Altitude: 1 437 ± 569, 324–1 948 m; annual rainfall: 721 ± 134, 484–900 mm; annual temperature (max. + min. /2): 15.0 ± 2.2, 12.2–18.0°C (N=8).

Habitat: No adequate quantitative assessment; in Suikerbosrand Nature Reserve: primarily sampled in cool S-facing montane grassland (> 1 880 m), not highveld grasslands (1 630–1 690 m); sampling records and DBRU collection records (2) only from sandy loam and sandy clay loam in grassland (1) and open woodland (1), but probably biased to grassland.

Food types: No quantitative assessment; sampled and collected by DBRU only from cattle dung.

Temporal activity: Flight activity in darkness primarily during the summer rainy season (Sept. to Mar.); attracted to light.

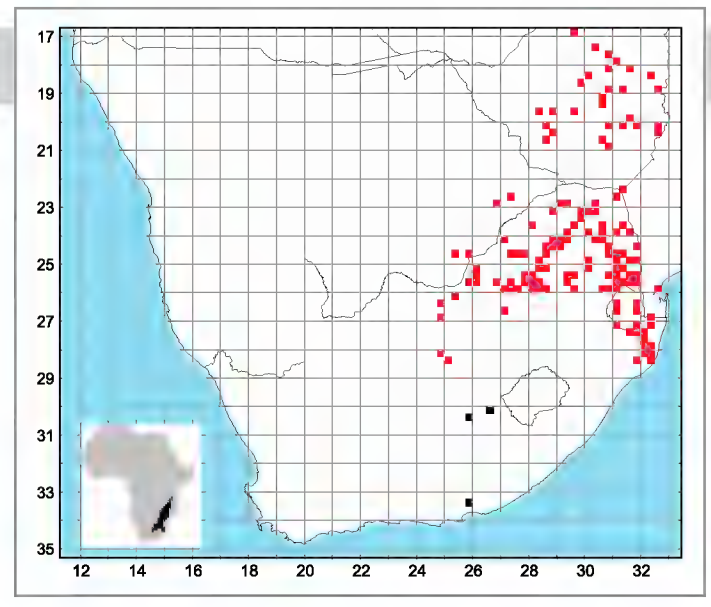
Bioregions South Africa: Centred along the highland margins of the Mesic Highveld Grassland (Gm), Drakensberg Grassland (Gd) and Sub-Escarpment Grassland (Gs) (Grassland Biome); also disturbed Sandstone Fynbos (FFs) (Fynbos Biome).

Assessment rationale: EOO = 41 240 km^2; AOO probably smaller reflected by patchy records, mostly in moist highland grassland units of the Grassland Biome in the summer rainfall region; transformation in vegetation units around known localities: Gm, 15%; Gd, 5%; Gs, 10–20%; somewhat Data Deficient (DD), but assessed as Least Concern (LC) on basis of wide range.

Conservation measures: Assessment of conservation status would be improved by a survey to determine additional locations, ecological associations, and possible effects of grassland modification; protected in Suikerbosrand Nature Reserve and uKhahlamba Drakensberg Park (World Heritage Site).

Copris denticulatus

Nguyen-Phung, 1988c



No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Shilouvane, près Leydsdorp' [Shiluvane near Leydsdorp, Limpopo Province, South Africa].

Taxonomy: Accepted Group 26 species; sexually dimorphic (head, prothoracic disc), prominence of characters varies with body size.

Distribution: Widespread in moist savannas of SE Africa: N South Africa, E Botswana, Zimbabwe, Mozambique, Tanzania; in Tanzania, range overlaps with the closely related *C. fallaciosus* Gillet, 1907, whose range extends to Uganda, Kenya, Somalia, Ethiopia; black squares are questionable outlier localities.

Locality data (mean ± SD, range): Altitude: 927 ± 437, 9–1 850 m; annual rainfall: 690 ± 151, 383–1 177 mm; annual temperature (max. + min. /2): 19.6 ± 1.9, 13.4–25.2°C (N=182).

Habitat: On Gauteng bushveld: strong bias to finer-grained soils, sandy clay loam (30), deep sand (3) in a range of vegetation types, grassland (10), open woodland (4), shaded thickets (19); not supported by DBRU collection records: clay (7), sandy clay loam (8), sandy loam (19), sand (15) in grassland/pasture (21), shrubland (8), open woodland (8), forest (2), also crop fields (2).

Food types: No quantitative data; DBRU collection records from ruminant herbivore dung: cattle (61), buffalo (3) far outweigh those from monogastric herbivore dung: elephant (4), square-lipped (white) rhinoceros (1), warthog (1).

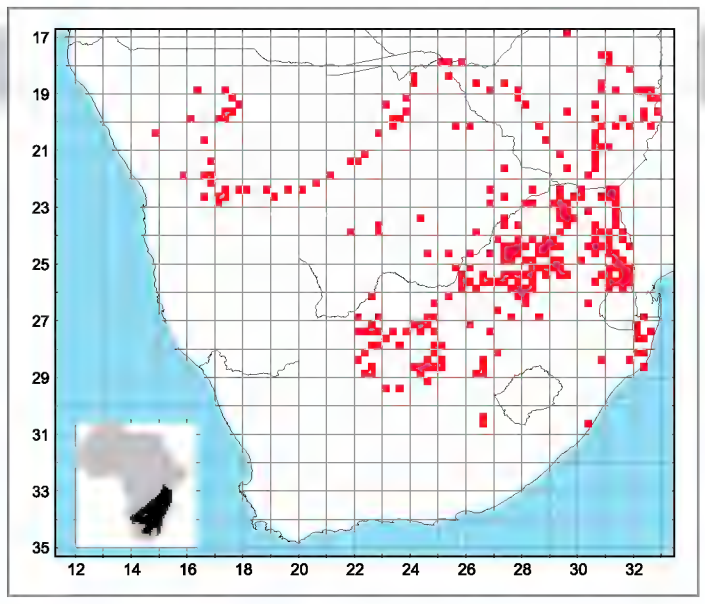
Temporal activity: Flight activity in darkness during the summer rainy season (Oct. to May); on Gauteng bushveld: seasonal peak in early summer (Nov., Dec.); attracted to light; bias to colonisation of older dung (18%, 1–2 day old dung; 63%, 2–4 day).

Ecoregions Botswana, Zimbabwe: Centred on Southern African Bushveld (AT0717), Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Mainly in the Central Bushveld (SVcb), Mopane (SVmp) and Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 940 275 km^2; widely distributed in farmland where it is readily attracted to cattle dung, often in open vegetation; therefore, perhaps not seriously threatened in the South African part of its range where transformation through cultivation varies from 0 to 58% (SVl), 2–49% (SVcb), 0–20% (SVmp); assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by further quantitative ecological data to resolve apparent conflicts between quantitative and qualitative results; protected in the Kruger National Park (South Africa).



Copris elphenor

Klug, 1855

= *Copris laticornis* Boheman, 1857

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *C. elphenor*: 'Sena' [Central Mozambique]; *C. laticornis*: 'Caffraria interiori' [interior of SE South Africa].

Taxonomy: Accepted Group 23 species; sexually dimorphic (head, prothoracic disc), prominence of characters varies with body size.

Distribution: Widespread in dry savanna from S to E Africa: N South Africa, N Namibia, Botswana, Zimbabwe, Malawi, Mozambique, S Angola, S Democratic Republic of the Congo (DRC), Zambia, Tanzania, S Kenya, possibly Somalia; West African records are certainly errors.

Locality data (mean ± SD, range): Altitude: 972 ± 425, 0–1 998 m; annual rainfall: 581 ± 188, 214–1 415 mm; annual temperature (max. + min. /2): 20.0 ± 2.1, 14.5–26.1°C (N=420).

Habitat: On Gauteng bushveld: strong bias to coarse-grained soils in relatively open vegetation, sand (247), sandy clay loam (44), grassland (127), open woodland (148), shaded thickets (16); similar patterns at Bushlands Halt: sand (182), clay loam (23), grassland (199), dense woodland (6); also supported by DBRU collection records: clay (5), sandy clay loam (25), sandy loam (56), sand (72) in pasture/grassland (53), shrubland (34), open woodland (50), forest (2), also crop fields (3).

Food types: On Gauteng bushveld: strong bias to dung of ruminant herbivores (cattle: 32) rather than that of monogastric herbivores (horse: 10), omnivores (pig: 3) or carrion (0); similar at Phalaborwa: dung of cattle (72), elephant (14), pig (1); DBRU collection records, ruminant herbivore dung: cattle (153), buffalo (6), wildebeest (3), monogastric herbivore dung: elephant (18), rhinoceros (6), donkey (1), horse (3); also baboon (2).

Temporal activity: Flight activity in darkness, primarily during the summer rainy season (Aug, Oct. to May); on Gauteng bushveld: seasonal peak, early to mid-summer (Oct. to Jan.) tailing off into late summer (Feb. to Apr.); flight activity peak 1–2 hours after nightfall (20:00–22:00); attracted to light; at Phalaborwa: much greater activity on a mild evening following heavy rainfall (78) than on a cool evening following light rain (3) or a hot evening under dry conditions (4); biased to colonisation of fresh dung (0–1 day: 56%, 1–3 days: 32%,).

Ecoregions Namibia, Botswana, Zimbabwe: Kalahari Xeric Savanna (AT1309), Southern African Bushveld (AT0717), Zambezian and Mopane Woodlands (AT0725), Southern Miombo Woodlands (AT0719), Angolan Mopane Woodlands (AT0702), Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian Baikiaea Woodlands (AT0726).

Bioregions South Africa: Centred on the Eastern Kalahari Bushveld (SVk), Central Bushveld (SVcb), Mopane (SVmp) and Lowveld (SVl) (Savanna Biome); some records in Dry Highveld Grassland (Gh) (W Grassland Biome); marginal occurrence in five other bioregions.

Assessment rationale: EOO = 3 968 635 km^2; widespread in farmland where it is occurs in both grassland and open woody vegetation with association biased to cattle dung; tolerance of open vegetation may reduce impact of habitat transformation over NE part of range in South Africa: 0–58% (SVl), 2–49% (SVcb), 0–20% (SVmp); assessed as Least Concern (LC).

Conservation measures: None required owing to wide occurrence, tolerance of open vegetation and ecological suitability for farm livestock; protected in Kruger National Park (South Africa).

Copris evanidus

Klug, 1855

= *Copris modestus* Boheman, 1857
= *Copris orphanus* Guérin-Méneville, 1847, *sensu* Péringuey, 1901

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *C. evanida*: 'Sena' [Central Mozambique]; As *C. modesta*: 'Caffraria tota' [all SE South Africa]; *C. orphanus sensu* Péringuey, 1901: 'Southern Rhodesia (Victoria Falls), Mozambique (Lourenço-Marquez)' [Zimbabwe, S Mozambique].

Taxonomy: Accepted Group 40 species; sexually dimorphic (head, prothoracic disc), prominence of characters varies with body size.

Distribution: Widespread in dry savanna along the E seaboard of Africa: N South Africa, E Botswana, Zimbabwe, Mozambique, Tanzania, Kenya; also cited from Uganda, Ethiopia.

Locality data (mean ± SD, range): Altitude: 802 ± 401, 55–1 762 m; annual rainfall: 564 ± 130, 304–909 mm; annual temperature (max. + min. /2): 20.6 ± 1.8, 15.9–25.7°C (N=217).

Habitat: In uMkhuze Game Reserve: extreme bias to finer-grained soils, sandy clay loam /clay (20), deep sand (0); on Gauteng bushveld: bias less extreme, sandy clay loam (22), deep sand (11) with a slight bias to open vegetation, grassland (20), open wood/thicket (13); partly supported by DBRU collection records: clay (2), sandy clay loam (12), sandy loam (37), sand (25) in grassland pasture (21), shrubland (10), open woodland (39).

Food types: At Phalaborwa: bias to elephant dung (11), few on cattle (1) and pig dung (0); in Botswana: bias to elephant dung (8), few on sheep (1), pig, cattle dung and carrion (0); DBRU collection records on ruminant herbivore dung: cattle (84), buffalo (3), wildebeest (2), monogastric herbivore dung: elephant (17), rhinoceros (2), zebra (1), also on baboon dung (1).

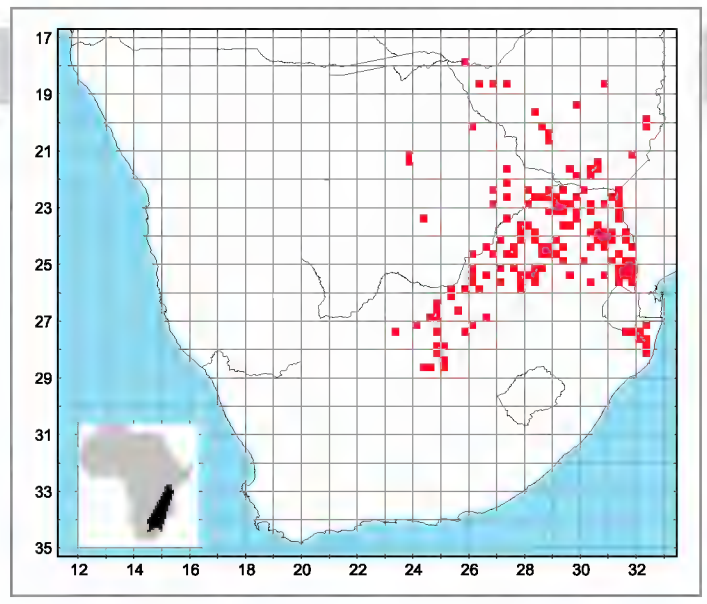
Temporal activity: Flight activity in darkness, primarily in the summer rainy season (Aug., Oct. to Apr.); on Gauteng bushveld: seasonal peak early to mid-summer (Oct. to Jan.) tailing off in late summer (Feb. to Apr.); attracted to light.

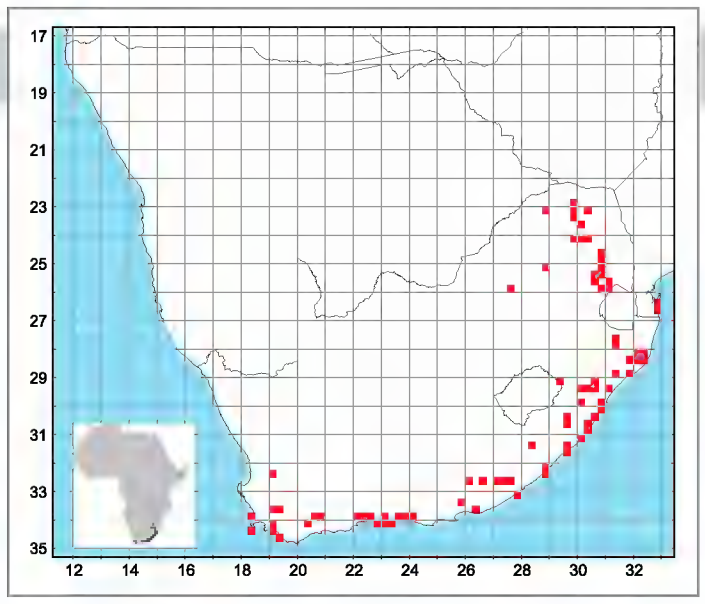
Ecoregions Botswana, Zimbabwe: Centred on Southern African Bushveld (AT0717), Zambezian and Mopane Woodlands (AT0725); also E margins of Kalahari Xeric Savanna (AT1309).

Bioregions South Africa: Centred on the Eastern Kalahari Bushveld (SVk), Central Bushveld (SVcb), Mopane (SVmp) and Lowveld (SVl) (Savanna Biome), with some records in the N of the Dry Highveld Grassland (Gh) (W Grassland Biome).

Assessment rationale: EOO = 2 357 905 km^2; possible bias to elephant dung may result in lower population densities over much of the species range; but remains extant using other dung types; apparently shows similar frequency in both grassland and open woodland whereas results for possible soil bias are inconclusive; widespread in both reserves and farmland; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by conclusive quantitative data on soil and food associations; protected in various reserves including the Kruger National Park and uMkhuze Game Reserve (South Africa).





Copris fidius

(Olivier, 1789)

= *Scarabaeus plutus* Fabricius, 1794
= *Copris* (*Paracopris*) *bihamatus* Balthasar, 1965a

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Scarabaeus fidius*: 'l'Amérique méridionale' [erroneously ascribed to Central America]; *S. plutus*: 'India orientali' [erroneously ascribed to eastern India]; *C. bihamatus*: 'Südafrika, Kapland (ohne nähere fudortangabe)' [South Africa, Cape (without more detailed place of origin)].

Taxonomy: Accepted Group 3 species; sexually dimorphic (head, prothoracic disc), prominence of characters varies with body size.

Distribution: Dual distribution pattern; one along entire S and E coastline, South Africa to S Mozambique; the other parallel along lower part of mountain escarpment diverging inland in NE South Africa; also in Cederberg (Western Cape) and N edge of Highveld; Namibia and Democratic Republic of the Congo (DRC) citations are certainly errors.

Locality data (mean ± SD, range): Altitude: 650 ± 571, 0–2 194 m; annual rainfall: 755 ± 222, 264–1 171 mm; annual temperature (max. + min. /2): 17.6 ± 2.3, 11.0–22.4°C (N=110).

Habitat: No quantitative assessment of soil type association; in the Wolkberg: extreme bias to shaded forest (55.6), grassland (0.6); similar in Ithala Game Reserve: Ntshondwe forest (32), open woodland (2), grassland (0); similar in Vernon Crookes Nature Reserve: forest (16), grassland (0); in the Wolkberg: favours lower altitudes, 900–1 000 m (15.6), 1 500–1 550 m (0.9); DBRU collection records on both finer and coarse-grained soils, sand (3), sandy clay loam (4) in grassland/pasture (4), woodland/forest (6).

Food types: In the Wolkberg: equally attracted to dung of ruminant herbivores (cattle: 67.1) and omnivores (pig: 50.6); DBRU collection records: primarily from dung of cattle (12), also monogastric herbivores, elephant (1), human/cattle dung mix (2).

Temporal activity: Flight activity in darkness, primarily in the summer rainy season in the NE part of the range (Oct. to May); spring activity (Sept.) in the winter rainfall region; attracted to light.

Ecoregions Mozambique: Maputaland Coastal Forest Mosaic (AT0119).

Bioregions South Africa: Primarily associated with scattered forest patches throughout most of the Afrotemperate, Subtropical and Azonal Forests Biome (FO); rare in Northern Afrotemperate Forest (FOz 2); none in Dune (FOz 8) and Azonal Forest (FOa).

Assessment rationale: EOO = 116 200 km^2; widespread along the entire E seaboard of South Africa where it is associated with forest patches; although forest clearance would radically reduce population density, known transformation of forest patches is low (5–6%), even though the original extent of many is unknown; currently assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on soil associations; protected in many game, forest and nature reserves including Lekgalameetse, Ithala, Hluhluwe–iMfolozi, Ngome, Vernon Crookes and Tsitsikamma (South Africa).

Copris gracilis

Waterhouse, 1891

= *Copris orphanus* Guérin-Meneville, 1847, *sensu* Ferreira, 1958b

Global: LC
Endemic: Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *C. gracilis*: 'Caffraria' [?southern Africa, see Taxonomy]; *C. orphanus sensu* Ferreira: 'Okahandja' [Namibia].

Taxonomy: Accepted Group 39 species, but status requires re-investigation; N Namibian distribution is at odds with 'Caffraria' type locality unless the term was used as a generality for southern Africa rather than in a more restricted sense for SE South Africa; differences to the closely related, SE to E African, *C. evanidus* Klug require validation; sexually dimorphic (head, prothoracic disc), prominence of characters varies with body size.

Distribution: Dry to arid savanna: northern plateau of Namibia.

Locality data (mean ± SD, range): Altitude: 1 394 ± 243, 799–1 998 m; annual rainfall: 340 ± 88, 125–549 mm; annual temperature (max. + min. /2): 19.3 ± 1.6, 16.9–23.0°C (N=54).

Habitat: No quantitative assessment; DBRU collection records: sandy clay loam (6), sandy loam (11), sand (10), mainly in woody vegetation: open woodland (15), shrubland (10), grassland (2).

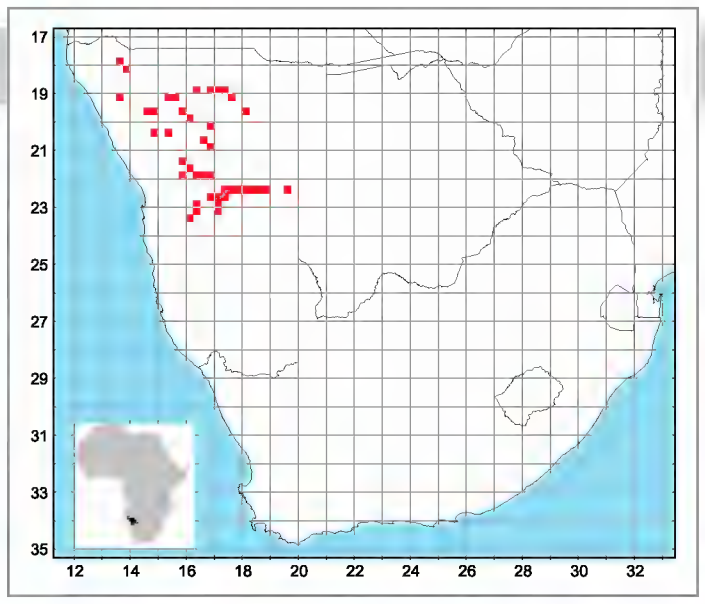
Food types: No quantitative assessment; DBRU collection records: mostly on cattle dung (25) with a few records from horse (2), zebra (1) and elephant (1) dung.

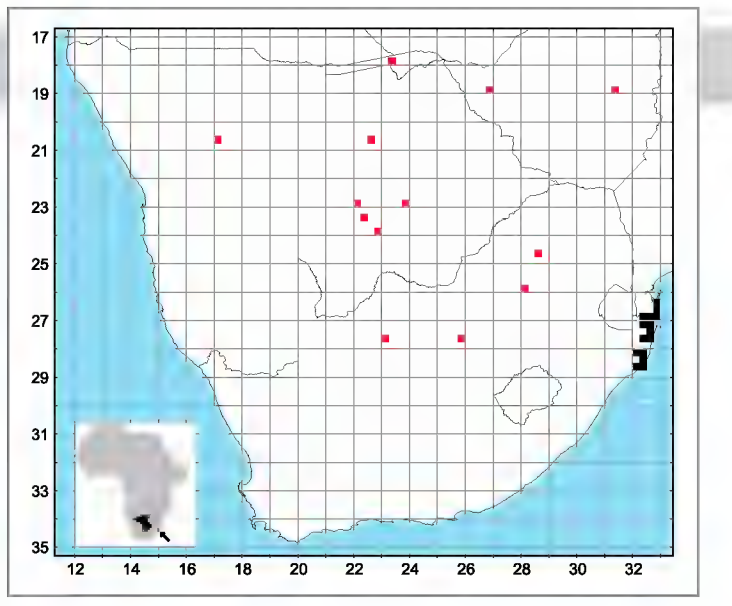
Temporal activity: Flight activity in darkness in the late summer rainy season (Dec. to Apr.).

Ecoregions Namibia: Centred on S Angolan Mopane Woodlands (AT0702), N Kalahari Xeric Savanna (AT1309) and central Namibian Savanna Woodlands (AT1316).

Assessment rationale: EOO = 168 350 km²; probably not under threat due to widespread occurrence in woodland savannas on farmland where it colonises cattle dung; assessed as Least Concern (LC) rather than Data Deficient (DD).

Conservation measures: Taxonomic issues need to be resolved; assessment of conservation status would be improved by quantitative data on ecological associations; currently unknown if clearance of woodland would be detrimental to population density or if it might be influenced by particular dung type associations; protected in Etosha National Park (Namibia).





Copris inhalatus

Quedenfeldt, 1884

subsp. *inhalatus* (Quedenfeldt, 1884)
subsp. *perturbator* (Péringuey, 1901)
subsp. *grandis* Nguyen-Phung & Cambefort, 1986b
subsp. *sanctaeluciae* Nguyen-Phung & Cambefort, 1986b
subsp. *ngotto* Moretto, 2011

No synonyms

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

subsp. *sanctaluciae*

Type localities: *C. inhalatus*: 'Malange' [Angola]; lectotype: Quango [Angola]; as *C. perturbator*: 'Ovampoland (Evari River), Southern Rhodesia (no exact locality)' [N Namibia; Zimbabwe]; subsp. *grandis*: 'N.W. Rhodesia; N. of Broken Hill' [N of Kabwe, Zambia]; subsp. *sanctaeluciae*: 'St Lucia Estuary, Natal' [KwaZulu-Natal, South Africa]; subsp. *ngotto*: 'Centrafrique, Ngotto' [Ngotto, Central African Republic].

Taxonomy: Accepted Group 12 species comprising five subspecies; all are sexually dimorphic (head, prothoracic disc), prominence of characters varies with body size.

Distribution: Mega-Kalahari deep sands and E outliers; three subspp. in Central Zambia; S Tanzania; or N Angola, W Democratic Republic of the Congo (DRC) and Congo (Brazzaville); two subspp. in S; *sanctaeluciae*: Maputaland Centre of Endemism on coast of NE South Africa and SE Mozambique; *perturbator*: N Namibia, Botswana, N South Africa, Zimbabwe, SW Zambia.

Locality data (mean ± SD, range): subsp. *perturbator* (red squares): Altitude: 1 147 ± 169, 924–1 444 m; annual rainfall: 492 ± 142, 346–761 mm; annual temperature (max. + min. /2): 19.9 ± 1.7, 17.5–22.4°C (N=14). subsp. *sanctaeluciae* (black squares): Altitude: 34 ± 54, 0–273 m; annual rainfall: 831 ± 107, 682–1 004 mm; annual temperature (max. + min. /2): 22.0 ± 0.5, 20.5–22.5°C (N=27).

Habitat: No quantitative assessment of soil bias; DBRU collection records exclusively from sand in both subspp. (11); subsp *sanctaeluciae*: in Maputo Special Reserve: primarily grassland (18.6) not forest (0.5); similar across Richards Bay, post-mining, restoration gradient: grassland (42), woodland/forest (0); subsp. *perturbator*: no quantitative assessment; DBRU collection records only shrubland/open woodland (5).

Food types: No quantitative assessment; DBRU collection records from cattle (5) and elephant (1) dung.

Temporal activity: Flight activity in darkness during the summer rainy season (Oct. to Feb.) extending into the cooler season for the coastal subspp. (May to June).

Ecoregions Namibia, Botswana Zimbabwe, Mozambique: subsp. *sanctaeluciae*: Maputaland Coastal Forest Mosaic (AT0119); subsp. *perturbator*: Kalahari Xeric Savanna (AT1309), Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian Baikiaea Woodlands (AT0726); deep sand outliers in Southern Miombo Woodlands (AT0719).

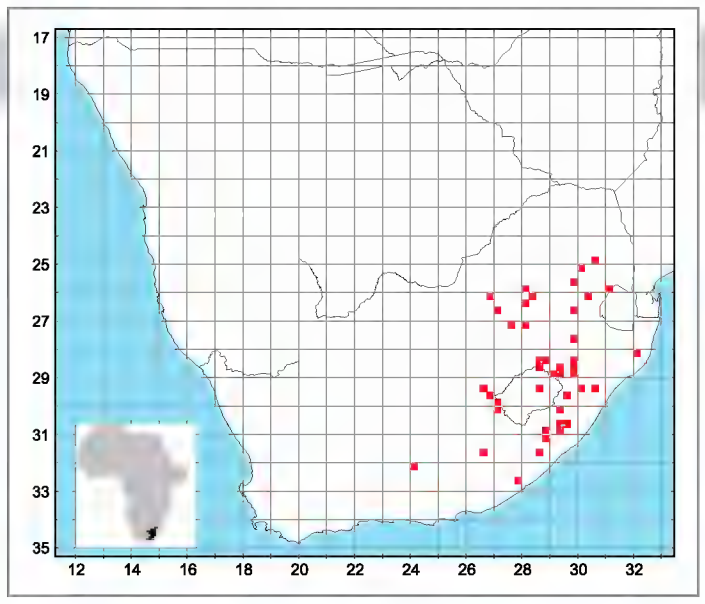
Bioregions South Africa: subsp. *sanctaeluciae*: Centred on N Indian Ocean Coastal Belt Biome (CB); subsp. *perturbator*: Centred on the Eastern Kalahari Bushveld (SVk) and sand outliers in Central Bushveld (SVcb) (Savanna Biome).

Assessment rationale: subsp. *perturbator*: EOO = 614 150 km^2; widespread, but uncommon, not recorded in a cross-Kalahari gradsect using

five different bait types, although most records have been made on cattle dung; much of its SW range used for grazing of domestic livestock; subsp. *sanctaeluciae*: EOO = 8 520 km^2; occupies a relatively small, but mostly protected range; both currently assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; reasons for low population density in subsp. *perturbator* should be investigated, particularly as most known records do not coincide with protected areas other than one in Hwange National Park (Zimbabwe); coastal subsp. *sanctaeluciae* protected in Maputo Special Reserve (Mozambique) and iSimangaliso Wetland Park (World Heritage Site) (South Africa).

subsp. *sanctaluciae*



Copris jacchoides

Nguyen-Phung & Cambefort, 1987

No synonyms

Global: LC
Endemic: RSA, Lesotho

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Transvaal' [N South Africa].
Taxonomy: Accepted Group 19 species; sexually dimorphic (head, prothoracic disc), prominence of characters varies with body size.
Distribution: Highveld and E coastal regions: South Africa.
Locality data (mean ± SD, range): Altitude: 1 430 ± 357, 117–1 983 m; annual rainfall: 724 ± 109, 355–958 mm; annual temperature (max. + min. /2): 15.3 ± 1.8, 12.1–21.3°C (N=52).
Habitat: No quantitative assessment; DBRU collection records primarily on finer-grained soils: clay (1), sandy clay loam (16), sandy loam (9), sand (1), in pasture/grassland (25); also fallow crop field (1).
Food types: No quantitative assessment; DBRU collection records entirely from cattle dung (33).
Temporal activity: Flight activity in darkness during the summer rainy season (Oct. to Mar.).
Bioregions South Africa: Moister E of Grassland Biome: Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs); marginal occurrence in W Dry Highveld Grassland (Gh) and four other bioregions.
Assessment rationale: EOO = 258 970 km^2; primarily centred in moist, cool, Highveld grasslands; at Carolina: recorded from improved Kikuyu pasture and fallow crop fields as well as natural *Themeda* grasslands, but numbers too limited to determine any habitat bias; transformation varies from 6 to 69% (Gm), 2–40% (Gs) across main range; assessed as Least Concern (LC) on basis of widespread occurrence.
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, particularly possible effects of grassland modification even though some records are from disturbed habitat; protected in Golden Gate National Park.

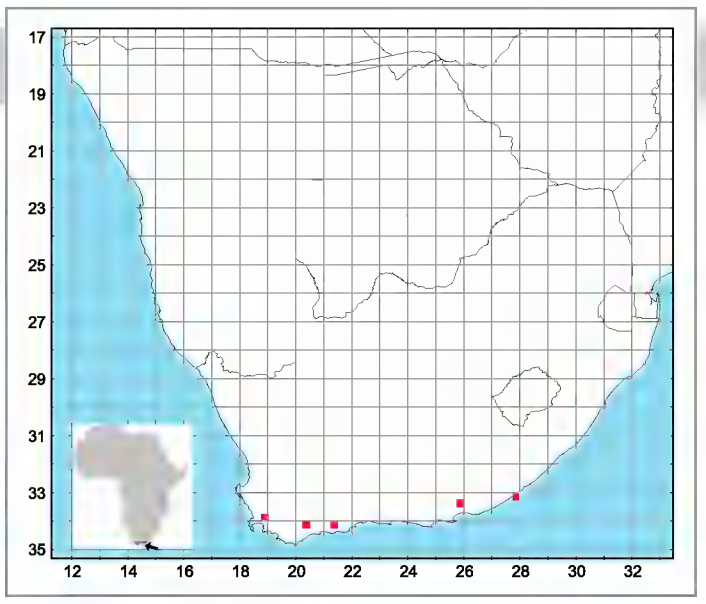
Copris jacchus

(Fabricius, 1775)

= *Scarabaeus oedipus* Fabricius, 1775
= *Copris laticornis* Wallengren, 1881

Global: NT
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: As *Scarabaeus jacchus*: 'Cap B. S.', lectotype, same type locality; *S. oedipus*: 'Cap B. S.', lectotype same type locality [all Cape of Good Hope, South Africa]; *C. laticornis*: Not stated.

Taxonomy: Accepted Group 19 species; sexually dimorphic (head, prothoracic disc), prominence of characters varies with body size.

Distribution: Low-altitude range along the drier parts of the S coast of South Africa in the winter and bimodal, spring/autumn, rainfall regions where natural vegetation is dominated by shrubland.

Locality data (mean ± SD, range): Altitude: 244 ± 178, 0–541 m; annual rainfall: 462 ± 140, 366–741 mm; annual temperature (max. + min. /2): 17.5 ± 1.1, 15.8–19.2°C (N=6).

Habitat: No quantitative assessment; only a single DBRU habitat observation on clay in open shrub/grassland.

Food types: No quantitative assessment; DBRU collection records from cattle (2) and buffalo (1) dung.

Temporal activity: Flight activity in darkness coinciding with warmer spring and autumn temperatures (Oct., May).

Bioregions South Africa: Vegetation units in Shale Renosterveld (FRs) (Fynbos Biome); Albany Thicket Biome (AT).

Assessment rationale: EOO = 9 990 km^2; known range < 20 000 km^2 with few known recent localities; natural lowland shrubland vegetation units are highly transformed in the W: FRs (Swartland, 90%; Mossel Bay, 58%), but less so in the E: AT (Sundays Thicket, 6%, but degraded by overgrazing; Great Fish Thicket, 3%); rather than Data Deficient (DD), tentatively assessed as possibly Near Threatened (NT) on basis of limited records from an often highly transformed region.

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, particularly an appraisal of its response to clearance of natural shrubland; without soil and vegetation association data it is difficult to determine if the AOO and population density would justify Least Concern (LC) status, the current tentative assessment as NT, or even Vulnerable (VU); protected in Addo Elephant National Park.

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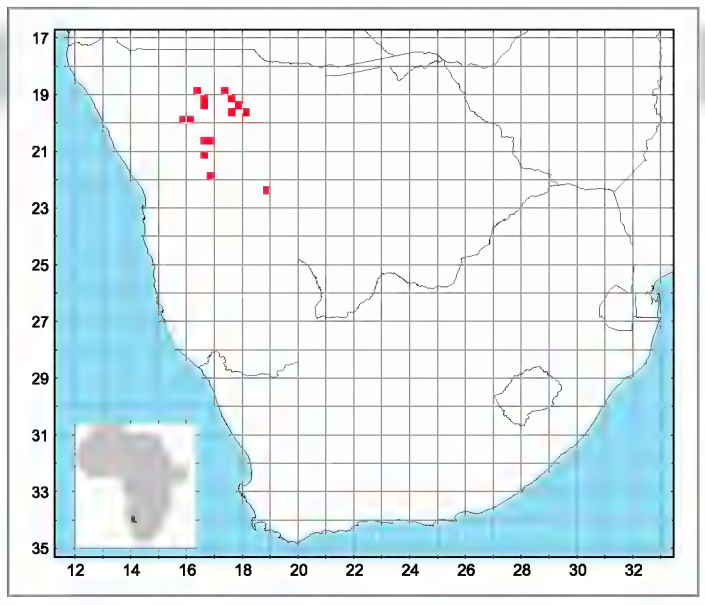


Copris laioides

Boucomont, 1932

No synonyms

Global: LC
Endemic: Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'Afrique de sud-ouest, Damaraland: Okanjande ou Okahandya sur le feuve Swakop' [Okanjande or Okahandja on the River Swakop, Namibia], lectotype, 'Okanjande, S.W. Afrika' [Mt Okonyande, Namibia].

Taxonomy: Accepted Group 20 species; sexually dimorphic (head, prothoracic disc), prominence of characters varies with body size.

Distribution: Dry savanna on the N Namibian plateau; reports from Zimbabwe, Democratic Republic of the Congo (DRC) require validation.

Locality data (mean ± SD, range): Altitude: 1 429 ± 151, 1 097–1 627 m; annual rainfall: 446 ± 64, 322–560 mm; annual temperature (max. + min. /2): 20.6 ± 1.2, 18.9–23.0°C (N=20).

Habitat: No quantitative assessment; DBRU collection records from various soil types: clay (2), sandy clay loam (4), sandy loam (2), sand (4), entirely in shrubland (5) or open woodland (8).

Food types: No quantitative assessment; DBRU records primarily on cattle dung (11), also horse (1) and donkey (1) dung.

Temporal activity: Flight activity in darkness in the late summer rainfall season (Dec. to Apr.).

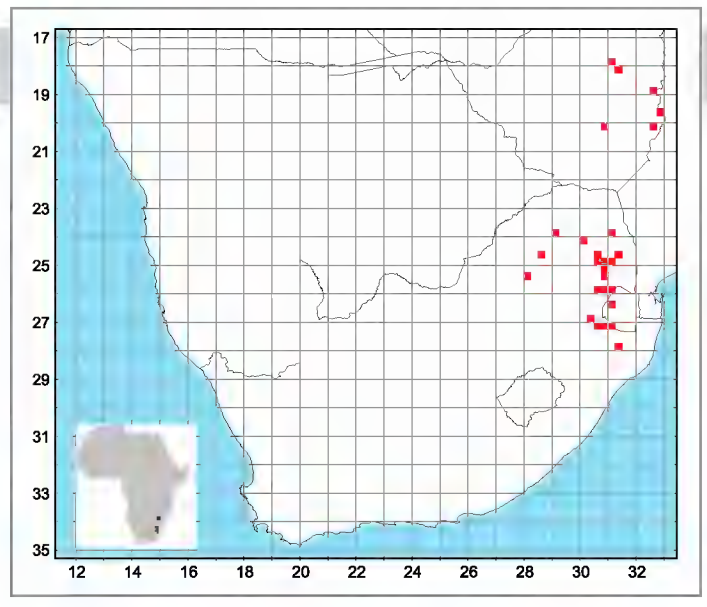
Ecoregions Namibia: S Angolan Mopane Woodlands (AT0702), N Kalahari Xeric Savanna (AT1309).

Assessment rationale: EOO = 49 485 km^2; potential threats currently limited as it is widespread on various soil types in farmland savanna where it colonises the dung of domestic livestock; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; possible effects of clearance of natural shrubland and woodland need to be investigated as no known localities coincide with protected areas.

Copris macer

Péringuey, 1901



No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Southern Rhodesia (Salisbury)' [Harare, Zimbabwe].

Taxonomy: Accepted Group 41 species; sexually dimorphic (head, prothoracic disc), prominence of characters varies with body size.

Distribution: Patchy occurrence on finer-grained soils in moist areas of SE Africa supporting open vegetation: N South Africa, Eswatini, Zimbabwe; also cited from Mozambique; report from Tanzania requires validation; that from Namibia possibly an error.

Locality data (mean ± SD, range): Altitude: 1 153 ± 361, 433–1 890 m; annual rainfall: 846 ± 150, 549–1 203 mm; annual temperature (max. + min. /2): 17.9 ± 2.1, 13.1–22.0°C (N=39).

Habitat: No quantitative assessment; DBRU collection records show bias to finer-grained soils: clay (1), sandy clay loam (7), sandy loam (7), sand (1), primarily in open vegetation: pasture/grassland (11), shrub/woodland (2).

Food types: No quantitative assessment; DBRU collection records entirely from ruminant dung: cattle (19), buffalo (1).

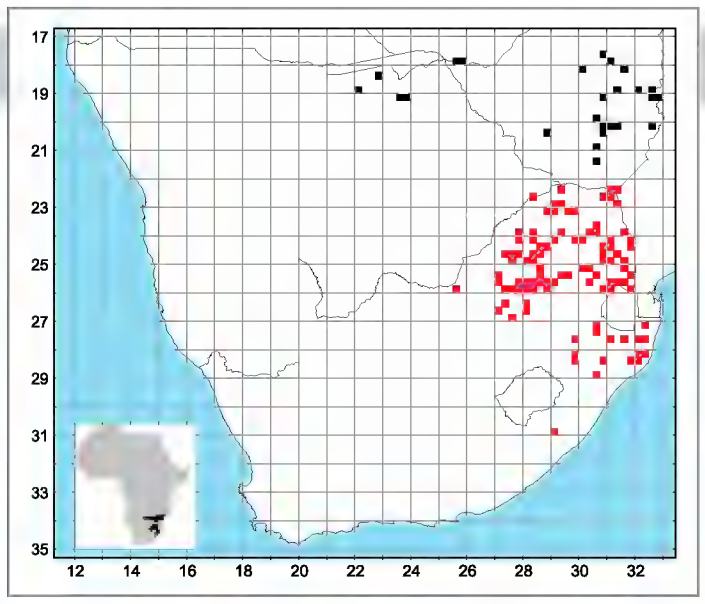
Temporal activity: Flight activity in darkness, primarily during the summer rainy season (Oct. to May).

Ecoregions Zimbabwe: E Southern Miombo Woodlands (AT0719), Eastern Zimbabwe Montane Forest Grassland Mosaic (AT1006).

Bioregions South Africa: Moist NE escarpment straddling the boundaries of N Mesic Highveld Grassland (Gm) (Grassland Biome) and Lowveld (SVl) (Savanna Biome); also moist patches in Central Bushveld (SVcb) (Savanna Biome).

Assessment rationale: EOO = 65 380 km² (underestimated); widespread in open vegetation of farmland, especially in moist grassland regions where it readily colonises cattle dung; assessed as Least Concern (LC) although transformation by cultivation and plantations in E Gm is 6–40%.

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; possible effects of grassland modification to improved pastures should also be investigated; protected in Lake Mutirikwe Game Reserve (Zimbabwe).



Copris mesacanthus

Harold, 1878

subsp. *mesacanthus* (Harold, 1878)
= *Copris similis* Balthasar, 1939a
subsp. *tranvaalensis* Nguyen-Phung, 1988

Global: LC
Endemic: RSA (subsp. *tranvaalensis*)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *C. mesacanthus*: 'N'Yassa', also lectotype: 'Nyassa' [inexact, Lake Malawi region]; as *Copris* (*Paracopris*) *similis*: 'Rhodesia, Monze, Chikuni Mission' [Zambia]; subsp. *tranvaalensis*: 'Transvaal, Shiloulvane, près Leydsdorp' [Shiluvane near Leydsdorp, Limpopo Province, South Africa].

Taxonomy: Accepted Group 1 species treated as two subspecies, both showing sexual dimorphism (head, prothoracic disc); prominence of characters varies with body size.

Distribution: Essentially, restricted to SE Africa; subsp. *tranvaalensis* (red squares): N South African savannas; subsp. *mesacanthus* (black squares): savannas of N Botswana, Zimbabwe, Zambia, Malawi, Mozambique.

Locality data (mean ± SD, range): subsp. *tranvaalensis*: Altitude: 944 ± 449, 46–1 899 m; annual rainfall: 670 ± 137, 304–1 040 mm; annual temperature (max. + min. /2): 19.4 ± 2.2, 13.1–24.5°C (N=133) | subsp. *mesacanthus*: Altitude: 894 ± 443, 0–1 640 m; annual rainfall: 791 ± 258, 427–1 623 mm; annual temperature (max. + min. /2): 20.9 ± 2.5, 17.1–26.1°C (N=34)

Habitat: subsp. *tranvaalensis*: On Gauteng bushveld: associated with finer-grained soils, sandy clay loam (95), deep sand (2) in more open vegetation, grassland (38), open woodland (51), shaded thickets (8); supported by limited DBRU collection records: sandy clay loam (6), sandy loam (4), sand (2) in grassland/pasture (4), shrub/woodland (8).

Food types: subsp. *tranvaalensis*: No adequate quantitative, data; DBRU collection records on various dung types: monogastric herbivore: elephant (4), rhinoceros (2), horse (1), ruminant herbivore: cattle (9), buffalo (2).

Temporal activity: subsp. *tranvaalensis*: Flight activity during darkness, primarily in the summer rainy season (Oct. to May); on Gauteng bushveld; activity commences early summer (Oct., Nov.) with a midsummer peak (Dec. to Feb.) tailing off into late summer (Mar., Apr.); attracted to light.

Ecoregions Botswana, Zimbabwe: subsp. *mesacanthus*: N Zambezian and Mopane Woodlands (AT0725), Southern Miombo Woodlands (AT0719); marginal in three other ecoregions.

Bioregions South Africa: subsp. *tranvaalensis*: Centred on Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome) with some records overlapping into the margins of three bioregions of the Grassland Biome.

Assessment rationale: subsp. *mesacanthus*: EOO = 378 400 km² | subsp. *tranvaalensis*: EOO = 223 300 km²; AOO perhaps limited by finer-grained soil association, but widespread in both reserves and farmland where it is found in both unshaded grassland and open woodland vegetation on the dung of farm livestock; assessed as Least Concern (LC).

Conservation measures: subsp. *tranvaalensis*: Assessment of conservation status would be improved by quantitative data on food associations; protected in uMkhuze Game Reserve and Kruger National Park (South Africa).

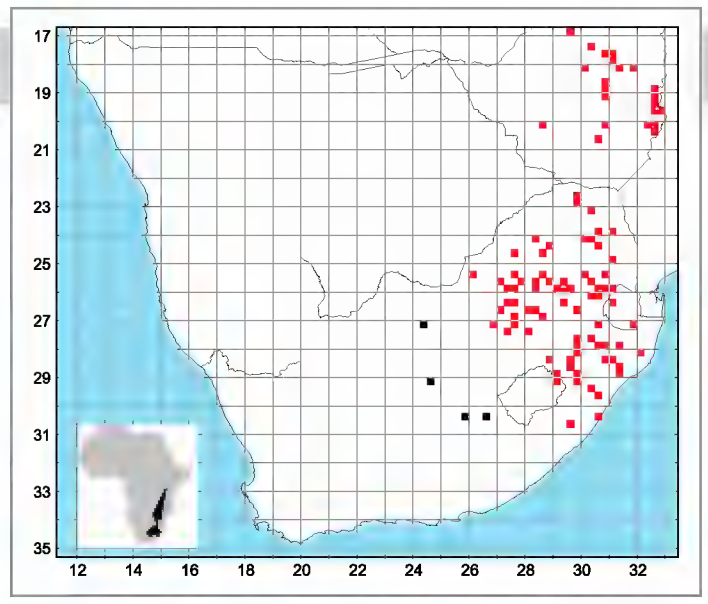
Copris obesus

Boheman, 1857

= *Copris contractus* Péringuey, 1901 (? *pars*)
= *Copris misellus* Péringuey, 1901

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: As *C. obesa*: 'prope fluvium Limpopo' [close to Limpopo River, southern Africa]; *C. contractus*: 'Cape Colony (Uitenhage, Graham's Town, Humansdorp, East London), Transvaal (Boksburg), Southern Rhodesia (Enkeldoorn, Buluwayo)' [South Africa; Zimbabwe]; *C. misellus*: 'Natal (Durban, Estcourt), Southern Rhodesia (Buluwayo, Salisbury), Transvaal (Waterberg, Potchefstroom)' [South Africa, Zimbabwe].

Taxonomy: Accepted Group 31 species but *C. contractus*: 'Cape Colony' material probably misidentified; secondary type of *C. misellus* from Durban (currently a valid species) in Iziko South African Museum appears to be a minor female specimen of *C. obesus*; sexually dimorphic (head, prothoracic disc), prominence of characters varies with body size.

Distribution: Moist grassland and savanna: SE to East Africa: Lesotho, South Africa, Zimbabwe, Mozambique, Zambia, Tanzania, Kenya; black squares are questionable localities.

Locality data (mean ± SD, range): Altitude: 1 237 ± 348, 273–2 392 m; annual rainfall: 752 ± 139, 377–1 160 mm; annual temperature (max. + min. /2): 17.7 ± 2.1, 9.9–23.3°C (N=131).

Habitat: No adequate quantitative assessment; in Abe Bailey Nature Reserve: grassland (52), open woodland (34); at Carolina: natural grassland (19) fallow crop field (7), improved Kikuyu grass pasture (4); DBRU collection records indicate bias to coarse-grained soils: clay (1), sandy clay loam (5), sandy loam (13), sand 13), and open vegetation: pasture/grassland (21), shrubland (4), open woodland (5).

Food types: No quantitative assessment; DBRU collection records primarily from ruminant herbivore dung: cattle (51), buffalo (1), few from monogastric herbivore dung: rhinoceros (2), zebra (1).

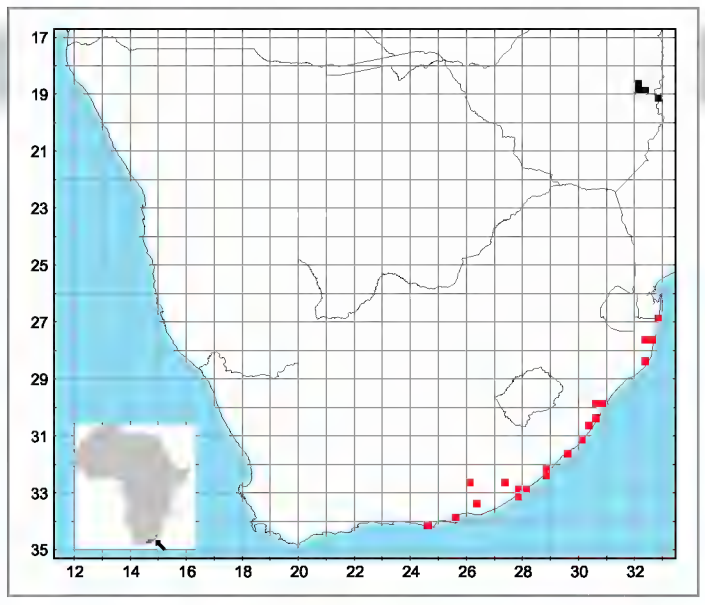
Temporal activity: Flight activity in darkness, primarily in the summer rainy season (Oct. to May).

Ecoregions Zimbabwe: Centred on Eastern Zimbabwean Montane Forest Grassland Mosaic (AT1006), Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Centred on warmer and moister vegetation units in N Mesic Highveld Grassland (Gm) and Sub-Escarpment Grassland (Gs) (Grassland Biome); also W Lowveld (SVl) and S Central Bushveld (SVcb) plus N Sub-Escarpment Savanna (SVs) (Savanna Biome).

Assessment rationale: EOO = 1 252 590 km² (gross estimate); widespread in farmland where it is attracted to the dung of domestic livestock in partially shaded and unshaded vegetation; habitat modification in grassland may reduce population density; transformation extensive across South African range (Gs, 3–50%; Gm, 6–67%; 0–58% (SVl), 2–49% (SVcb)), but assessed as Least Concern (LC) on basis of large range.

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; effects of grassland modification should be further investigated; protected in various nature reserves: Abe Bailey, Suikerbosrand, Rustenburg (South Africa).



Copris orion

Klug, 1835

subsp. *orion* (Klug, 1835)
subsp. *centralis* Gillet, 1908
subsp. *caffer* Gillet, 1908
subsp. *overlaeti* (Balthasar, 1961b)

No synonyms

Global: LC
Endemic: RSA (subsp. *caffer*)

J	A	S	O	N	D	J	F	M	A	M	J

subsp. *caffer*

Type localities: *C. orion*: 'Senegal', neotype, same locality; as *C. orion* var. *centralis*: 'Congo ou d'Afrique orientale' [Democratic Republic of the Congo (DRC) or East Africa]; as *C. orion* var. *caffer*: 'Afrique austral' [South Africa]; *C. overlaeti*: 'Lulua: Muteba' [Democratic Republic of the Congo (DRC)].

Taxonomy: Accepted Group 38 species comprising four described subspp.; sexually dimorphic (head, prothoracic disc); prominence of characters varies with body size.

Distribution: Three subspp. recorded from West (*orion*) or central Africa (*overlaeti*, *centralis*); subsp. *caffer* (red squares): moist, coastal, lowland distribution from N KwaZulu-Natal to E Eastern Cape, South Africa; unidentified further subsp. from E Zimbabwe (black squares).

Locality data (mean ± SD, range): subsp. *caffer*: Altitude: 189 ± 250, 0–984 m; annual rainfall: 806 ± 181, 430–985 mm; annual temperature (max. + min. /2): 19.4 ± 1.8, 15.7–22.4°C (N=23).

Habitat: subsp. *caffer*: No quantitative assessment; limited DBRU collection records on sand (1), sandy loam (2) sandy clay loam (1), entirely from open grassland (4) or scrub (1) vegetation.

Food types: subsp. *caffer*: No quantitative assessment; all DBRU collection records from cattle dung (5).

Diel activity: subsp. *caffer*: Flight activity in darkness in the summer rainy season (Nov. to Mar.).

Bioregions South Africa: subsp. *caffer*: Centred on Indian Ocean Coastal Belt across Albany Thicket to E edge of Fynbos Biomes.

Assessment rationale: EOO = 31 800 km^2 (subsp. *caffer*); fairly widespread, but largely restricted to the narrow coastal belt; apparent association with open vegetation and ready colonisation of cattle dung suggests limited threats due to a certain degree of adaptability to farmland conditions; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, particularly vegetation associations and possible effects of grassland modification; protected in Vernon Crookes Nature Reserve.

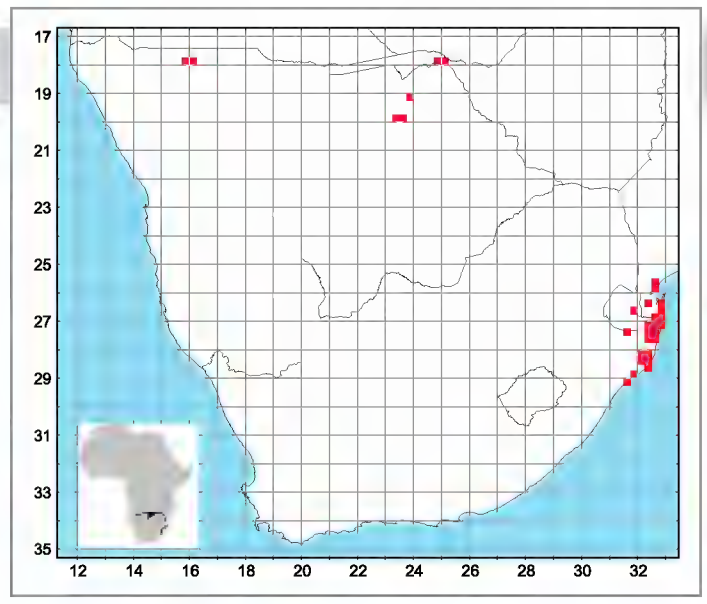
Copris puncticollis

Boheman, 1857

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: 'Caffraria interiori' [interior of SE South Africa].

Taxonomy: Accepted Group 40 species; sexually dimorphic (head, prothoracic disc), prominence of characters varies with body size.

Distribution: Grassland on SE coast deep sands: NE KwaZulu-Natal (South Africa) at least as far N as Beira (central Mozambique); also up Zambezi Valley following Zimbabwe/Zambia border to floodplains of Okavango (N Botswana), Kafue (Zambia) and Ovamboland (N Namibia).

Locality data (mean ± SD, range): Altitude: 245 ± 384, 0–1 094 m; annual rainfall: 778 ± 186, 428–1 275 mm; annual temperature (max. + min. /2): 22.3 ± 0.8, 20.4–24.6°C (N=43).

Habitat: At Bushlands Halt: strong bias to deep sands in grassland, sand (223), clay loam (8), grassland (217), dense woodland (14); on deep sands in Maputo Special Reserve: natural grassland (62), forest (2); on sand dunes at Richards Bay: early succession post-mining grassland (22), late succession woodland / natural dune forest (0); supported by DBRU collection records: sand (9), finer-grained soils (3), pasture/grassland (9), woody vegetation (4).

Food types: No quantitative assessment; DBRU collection records primarily on cattle dung (9), elephant dung (2).

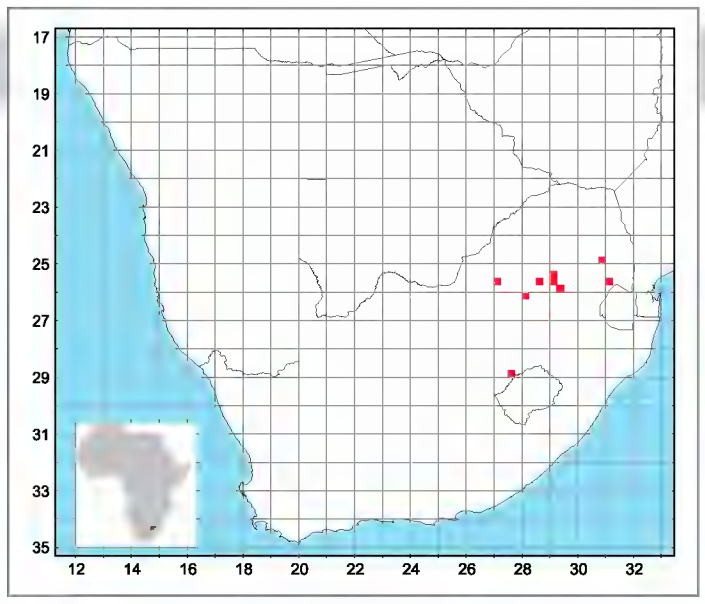
Temporal activity: Flight activity in darkness, primarily during the summer rainy season (Oct. to Apr.), but also in the cooler season along the warmer coast; bias to colonisation of fresh dung (63%, 0–2 day old).

Ecoregions Namibia, Botswana, Mozambique: Centred on grasslands: Maputaland Coastal Forest Mosaic (AT0119), Southern Zanzibar-Inhambane Coastal Forest Mosaic (AT0128); also in four isolated elements of Zambezian Flooded Grasslands (AT0907), Angolan Mopane Woodlands (AT0702).

Bioregions South Africa: Primarily in N Indian Ocean Coastal Belt Biome (CB) with marginal records in the adjoining S Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 211 185 km^2; widespread, but with AOO apparently centred on deep sands primarily in open grassland vegetation; occurrence on floodplains and in post-mining, early succession grassland suggests an adaptable species; much of the coastal range in South Africa and SE Mozambique is protected; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on food associations; protected in Tembe Elephant Park, Sileza Nature Reserve and iSimangaliso Wetland Park (World Heritage Site) (South Africa); Maputo Special Reserve (Mozambique); and Kafue National Park (Zambia).



Copris ritsemae

Harold, 1875

= *Copris victorini* Boheman, 1857, *sensu* Péringuey, 1901 (*pars*)

Global: DD (see IUCN Red List – DD)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *C. ritsemae*: 'Basutoland (Afric. austr.)' [Lesotho]; *C. victorini sensu* Péringuey (*pars*) (see Taxonomy): 'Transvaal (Pretoria, Johannesburg), Natal (Durban), Orange Free State (Parys)' [Gauteng, KwaZulu-Natal, Free State; South Africa], also 'Cape Colony (Knysna, Seymour)' [Eastern Cape].

Taxonomy: Accepted Group 18 species, but often confused with close relatives; type series of synonym probably includes two species plus *C. victorini*; Gauteng and Free State localities probably *C. ritsemae* Harold; KwaZulu-Natal locality may be *C. vrydaghi* Ferreira or *C. caelatus* (Fabricius); Eastern Cape localities probably true *C. victorini* Boheman; sexually dimorphic (head and prothoracic disc), prominence of characters varies with body size.

Distribution: Primarily recorded in moist grassland along N edge of Highveld: South Africa; disjunctions between N, NE and S records may be real or a collection artefact; S record close to Lesotho type locality.

Locality data (mean ± SD, range): Average altitude: 1 356 ± 362, 671–1 890 m; average annual rainfall: 724 ± 110, 619–996 mm; average annual temperature (max. + min. /2): 17.3 ± 2.3, 13.1–20.6°C (N=10).

Habitat: No quantitative assessment; limited DBRU collection records on sandy loam (1), sandy clay loam (1) in grassland/pasture (2).

Food types: No quantitative assessment; limited DBRU collection records on cattle dung (2).

Temporal activity: Diel periodicity unknown, but possibly diurnal like its close relative, *C. caelatus* (Fabricius); active primarily during the summer rainy season (Oct. to May).

Bioregions South Africa: Straddling N and E edges of Mesic Highveld Grassland (Gm) (Grassland Biome) and Savanna Biome (grassy areas in Central Bushveld (SVcb) and Lowveld (SVl)).

Assessment rationale: EOO = 18 840 km^2; long series recorded in Johannesburg (1905) and NW border of Lesotho (1970); more recent records suggest very low population density, perhaps, since much of known range coincides with highly transformed areas; fairly widespread, but ecologically poorly known; currently assessed as Data Deficient (DD).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, particularly possible effects of habitat transformation; also, a quantitative survey of the N Highveld is required to determine the full EOO and AOO; protected in Telperion and Rustenburg nature reserves.

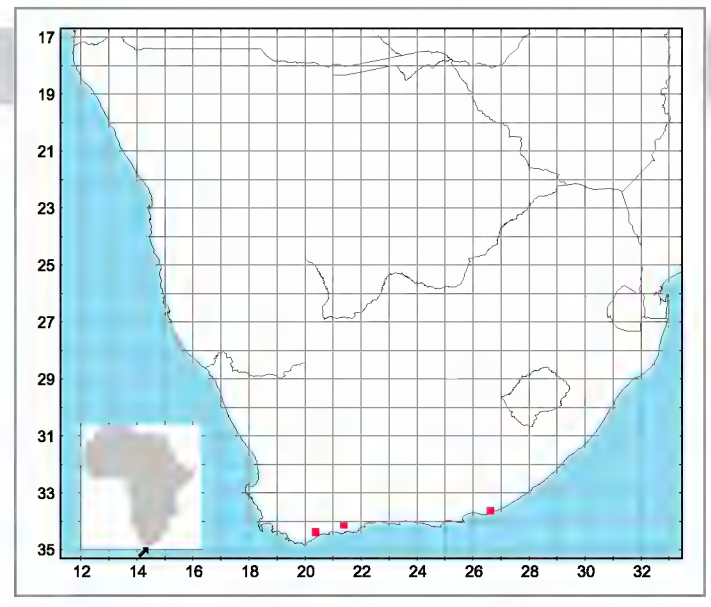
Copris sexdentatus

Thunberg, 1818

= *Copris lineatus* Wiedemann, 1823
= *Copris globulipennis* Waterhouse, 1891

Global: EN
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: *C. sexdentatus*: 'Majorem horum partem in Capite bonae spei collegi' [amongst material mostly collected in the Cape of Good Hope]; *C. lineata*: 'Prom. bon. sp.' [Cape of Good Hope]; *C. globulipennis*: 'Cape of Good Hope' [South Africa].

Taxonomy: Accepted Group 16 species; sexually dimorphic (head, prothoracic disc), prominence of characters varies with body size.

Distribution: Only three spot records available, S coastal lowlands of South Africa; bimodal rainfall region from E Western Cape to W Eastern Cape.

Locality data (mean ± SD, range): Altitude: 88 ± 84, 16–181 m; annual rainfall: 427 ± 67, 358–492 mm; annual temperature (max. + min. /2): 17.6 ± 0.5, 17.3–18.2°C (N=3).

Habitat: No quantitative assessment; presumably finer-grained soils in shrubland vegetation based on a recent record from Renosterveld.

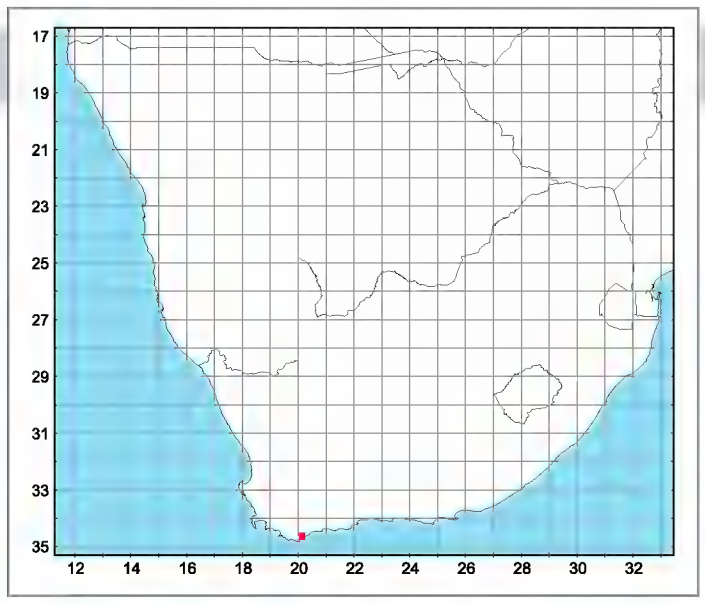
Food types: No quantitative assessment; unknown.

Temporal activity: Flightless and apterous; diel periodicity probably diurnal; observed walking on the soil surface during daytime; recent rediscovery during late winter / early spring, end of July.

Bioregions South Africa: W records: critically endangered Eastern Rûens Shale Fynbos (FRs 13) (Renosterveld Bioregion, Fynbos Biome); E record possibly inexact: Kowie Thicket (AT 8) (Albany Thicket Biome).

Assessment rationale: EOO = 3 945 km^2; represented by few specimens in collections; not recorded in the past 45 years by collectors from research groups or Gauteng museums, despite serial collecting in disturbed habitat within the species range; the recent rediscovery (2016) of one individual in undisturbed Renosterveld (FRs 13) may be the the only validated spot locality and the first record of the species for over a century; two other available old records possibly inaccurate, requiring validation; 80% transformation in FRs 13, mostly by arable farming; 7% in AT 8, but species occurrence requires validation; a range of < 5 000 km^2 at < 5 locations with only a single recent record justifies an EN category, possibly even CR, considering its flightless condition.

Conservation measures: To confirm threat level and conservation status of this species, a survey of surviving natural shrubland vegetation in lowland Renosterveld is essential; this should determine the current EOO, AOO as well as ecological associations; a survey of Albany Thicket is also necessary to validate or invalidate its occurrence in the Eastern Cape; now protected in Haarwegskloof Renosterveld Reserve; status unknown in patches of FRs 13 that are conserved in De Hoop Nature Reserve and Bontebok National Park.



Copris sphaeropterus

Harold, 1877b

No synonyms

Global: EN
Endemic: RSA

| J | A | S | O | N | D | J | F | M | A | M | J |

Type locality: 'Cap bon. spei.' [Cape of Good Hope, South Africa].
Taxonomy: Accepted Group 16 species; sexually dimorphic (head, prothoracic disc), prominence of characters varies with body size.
Distribution: Only one spot record available; S coastal lowlands of South Africa, winter rainfall region, Western Cape; published records further eastwards into the bimodal region, E Eastern Cape, remain unvalidated.
Locality data (average): Altitude: 152 m; annual rainfall: 422 mm; annual temperature (max. + min. /2): 16.4°C (N=1).
Habitat: Unknown, but presumably ecologically different from its close relative *C. sexdentatus* Thunberg, 1818, which has been recorded from a validated locality on finer-grained soils in shrubland of the Eastern Rûens Shale Renosterveld (FRs 13).
Food types: Unknown.
Temporal activity: Flightless and apterous; diel periodicity unknown, but possibly diurnal like the closely related *C. sexdentatus*; no dated material available.
Bioregions South Africa: Critically endangered Central Rûens Shale Fynbos (FRs 12) (Renosterveld, Fynbos Biome).
Assessment rationale: No EOO estimate possible; represented in collections by few specimens; only one available relatively exact spot locality on an old label; none recorded in the past 45 years by collectors from Gauteng museums or research groups despite serial collecting within the species range; transformation: FRs 12, 87% by cultivation; a range of < 5 000 km^2 at < 5 locations with no recent records justifies at least an assessment of Endangered (EN).
Conservation measures: A survey of surviving natural shrubland vegetation in lowland Renosterveld is essential to determine the ecological associations, level of threat and conservation status of this species; not known to be protected within any reserve, but a small amount of FRs 12 is conserved in Agulhas National Park.

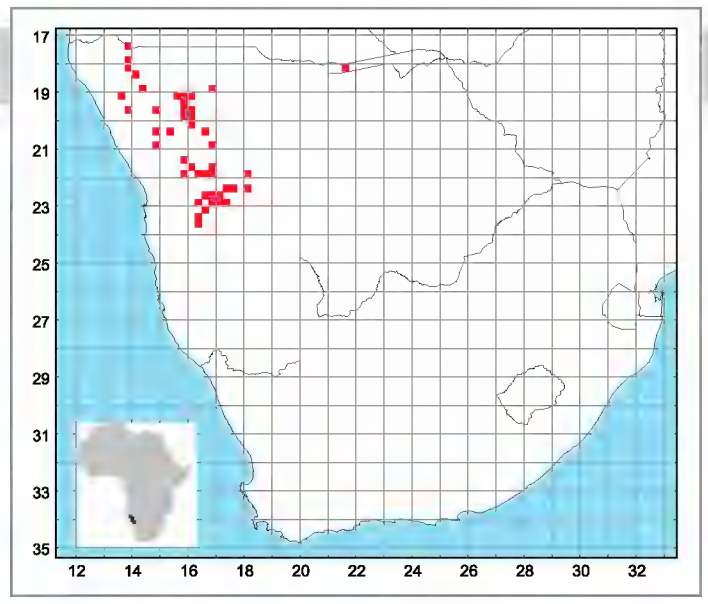
Copris subsidens

Péringuey, 1901

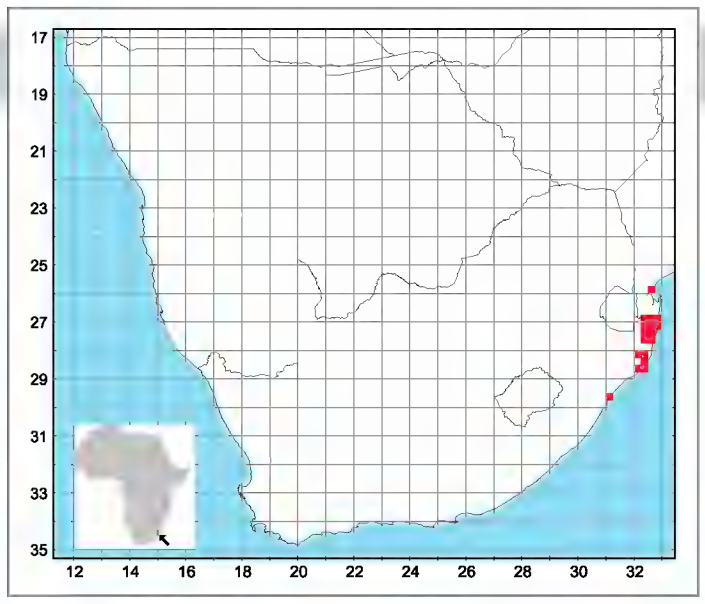
No synonyms

Global: LC
Endemic: Namibia

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: 'Damaraland' [N Namibia].
Taxonomy: Accepted Group 31 species; sexually dimorphic (head, prothoracic disc), prominence of characters varies with body size.
Distribution: Arid to dry savanna of the N Namibian Plateau with an isolated record from the Caprivi Strip.
Locality data (mean ± SD, range): Altitude: 1 366 ± 323, 608–1 998 m; annual rainfall: 340 ± 72, 171–540 mm; annual temperature (max. + min. /2): 19.1 ± 2.0, 15.7–23.0°C (N=58).
Habitat: No quantitative assessment; DBRU collection records on various soils: clay (1), sandy clay loam (13), sandy loam (14), sand (9), primarily in shrubland (16) and open woodland (17) with only two observations in grassland.
Food types: No quantitative assessment; DBRU collection records in farmland on cattle (23) horse (1) and donkey dung (1); also various dung types in Etosha NP: wildebeest (2), elephant (3), zebra (3).
Temporal activity: Flight activity in darkness in the late summer rainy season (Dec. to Apr.); attracted to light.
Ecoregions Namibia: S Angolan Mopane Woodlands (AT0702), N Kalahari Xeric Savanna (AT1309), central Namibian Savanna Woodlands (AT1316).
Assessment rationale: EOO = 105 070 km^2; widespread in farmland where it colonises the dung of domestic livestock; primarily recorded in natural shrubland and woodland although there is no quantitative support for such habitat bias; currently assessed as Least Concern (LC) on basis of large EOO.
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; it is necessary to investigate possible effects on population density of clearance of woody vegetation; protected in Etosha National Park.



Copris urus

Boheman, 1857

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'prope fluvium Limpopo' [close to Limpopo River, southern Africa; ?near the Indian Ocean river mouth].

Taxonomy: Accepted Group 48 species; sexually dimorphic (head, prothoracic disc), prominence of characters varies with body size.

Distribution: Known only from the deep coastal sands of the Maputaland Centre of Endemism, particularly in NE KwaZulu-Natal, South Africa, less frequently in drier SE Mozambique.

Locality data (mean ± SD, range): Altitude: 42 ± 56, 0–273 m; annual rainfall: 847 ± 116, 682–1 006 mm; annual temperature (max. + min. /2): 21.9 ± 0.5, 20.5–22.9°C (N=25).

Habitat: At Bushlands Halt: restricted to deep sands in both grassland and woodland, sand (77), clay loam (0), grassland (43), dense woodland (34); across a restoration gradient on coastal dunes at Richards Bay: mainly in early successional grassland (19) and open late successional woodland (5); rare in dense, early succession woodland (0) and natural dune forest (1); DBRU collection records only on sand (4).

Food types: No quantitative assessment; DBRU collection records on cattle (4) and elephant (1) dung.

Temporal activity: Flight activity in darkness, primarily in the summer rainy season (Oct. to Jan.), but also the cooler season (June, Aug.) owing to its warm coastal range; bias to colonisation of older dung (24%, 0–2 day old; 48%, 2–4 day).

Ecoregions Mozambique: Maputaland Coastal Forest Mosaic (AT0119).

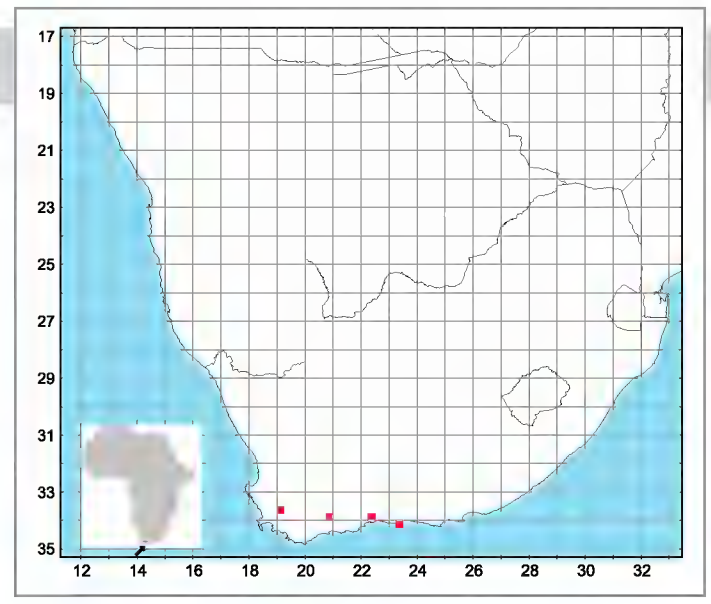
Bioregions South Africa: N Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 8 690 km^2; relatively small EOO in a region comprising a mosaic of soil and vegetation types; AOO would be smaller due to soil specialisation; possibly influenced by a bias to open vegetation at the cooler coast compared to a more generalist distribution between open and dense vegetation types in warmer inland situations; however, assessed as Least Concern (LC) rather than Vulnerable (VU) owing to the level of protection over much of its range.

Conservation measures: Assessment of conservation status would be improved by quantitative data on food associations; much of the EOO protected in the iSimangaliso Wetland Park (World Heritage Site) (South Africa); however, as regards the AOO, a more accurate assessment of the conservation status of this species might result from an investigation of the relative importance of vegetation types with increasing proximity to the coastline, particularly that of grassland on fossil lagoons.

Copris victorini

Boheman, 1857



No synonyms

Global: DD (see IUCN Red List – DD)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Caffraria meridionali….et ad Promont. Bonae Spei' [southern SE South Africa to Cape of Good Hope].

Taxonomy: Accepted Group 17 species; sexually dimorphic (head and prothoracic disc), prominence of characters varies with body size.

Distribution: Restricted to a small known range along the S coast and S coastal mountains of South Africa in the winter and bimodal rainfall regions.

Locality data (mean ± SD, range): Altitude: 437 ± 350, 0–822 m; annual rainfall: 425 ± 47, 363–465 mm; annual temperature (max. + min. /2): 16.1 ± 1.5, 14.4–18.0°C (N=4).

Habitat: No quantitative assessment; no soil type data, but known mainly from sandy bioregions; recorded in fynbos shrubland (top of Dutoitskloof Pass near Paarl).

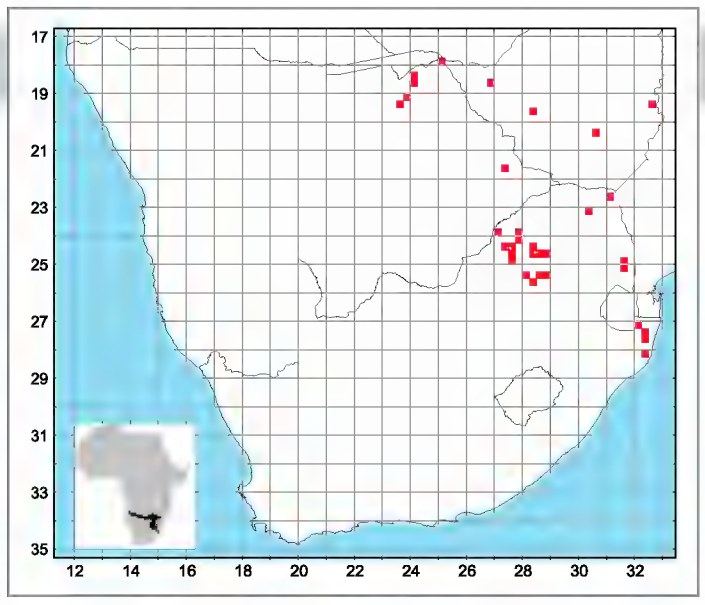
Food types: No quantitative assessment; recorded from a klipspringer midden (top of Dutoitskloof Pass near Paarl).

Temporal activity: Unknown, possibly diurnal like one other member of its species group; recorded in early summer (Nov., Dec.).

Bioregions South Africa: Vegetation units of Sandstone Fynbos (FFs), Granite Fynbos (FFg), and Shale Fynbos (FFr).

Assessment rationale: EOO = 2 100 km^2; currently assessed as Data Deficient (DD) due to limited data, but on the basis of a known range of < 5 000 km^2 and records from less than five locations, this species currently deserves Endangered (EN) status; however, there is low transformation around two data points in the extensively protected (78–86%) W vegetation units: Hawequas Sandstone Fynbos (FFs 10, 3%), South Langeberg Sandstone Fynbos (FFs 16, 4%); whereas there is high transformation in the E: Garden Route Granite Fynbos (FFg 5, 70%), Garden Route Shale Fynbos (FFh 9, >50%).

Conservation measures: To determine the conservation status of this species, a survey of S mountain and S coastal habitats is necessary to ascertain the full extent of its EOO and AOO, its ecological associations, and the number of occupied locations; protected in Grootvadersbosch Nature Reserve.



Copris vilhenai

Ferreira, 1962a

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Província de Angola: n.º ANG.: 10609, Marco de Canavezes (Membassoco), proximo da Central Hidroelectrica da Companhia de Acucar de Angola' [Membassoco, Angola].

Taxonomy: Accepted Group 41 species; sexually dimorphic (head, prothoracic disc), prominence of characters varies with body size.

Distribution: Patchy occurrence across extensive areas and smaller pockets of deep sands in N South Africa, N Botswana, S Angola, Zimbabwe, Mozambique.

Locality data (mean ± SD, range): Altitude: 867 ± 420, 55–1 516 m; annual rainfall: 630 ± 121, 430–1 136 mm; annual temperature (max. + min. /2): 20.8 ± 1.6, 17.2–25.2°C (N=43).

Habitat: In Gauteng (cited as *C. macer*): extreme association with coarse-grained soils, deep sand (19), sandy clay loam (0) in woody vegetation, grassland (1), open woodland (4), shaded thickets (14); partly supported by DBRU collection records: sand (12), sandy loam (7), clay (2) in grassland (2), shrub/woodland (17), forest (2).

Food types: In Botswana: bias to elephant (9) rather than cattle (2), pig, sheep dung or carrion (all 0); DBRU collection records shared between monogastric herbivore: elephant (7), rhinoceros (1), and ruminant herbivore dung: cattle (9), buffalo (2), wildebeest (1).

Temporal activity: Flight activity in darkness, primarily during the summer rainy season (Oct. to May) with additional cool season activity along the warmer coastline (July, Aug.); on Gauteng bushveld: seasonal peak during early summer (Oct. to Dec.).

Ecoregions Botswana, Zimbabwe: Southern African Bushveld (AT0717), Zambezian and Mopane Woodlands (AT0725), Zambezian Baikiaea Woodlands (AT0726); margins of two other ecoregions.

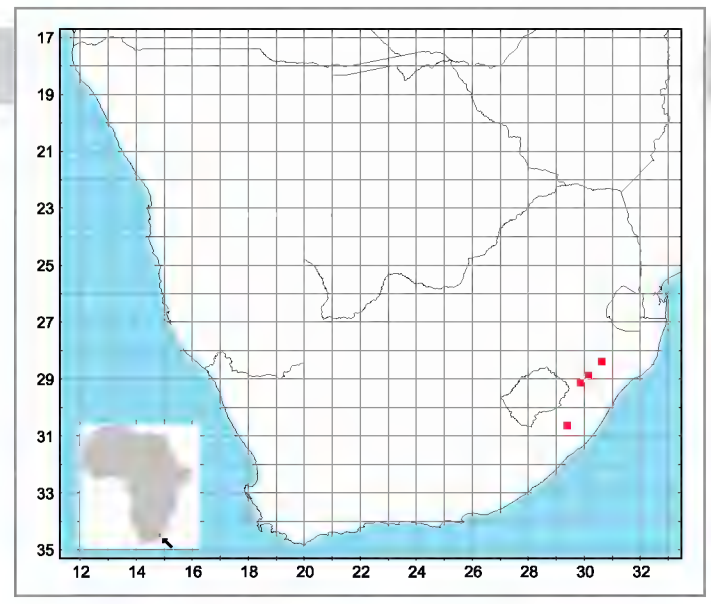
Bioregions South Africa: Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 677 310 km^2; AOO probably smaller due to sand specialisation; bias to monogastric dung presumably results in lower population density in farmland although it does colonise cattle dung; association with woody vegetation suggest its clearance would also reduce population density; transformation across South African range, 0–58% (SVl), 2–49% (SVcb); currently assessed as Least Concern (LC) on basis of widespread range.

Conservation measures: Assessment of conservation status would be improved by more comprehensive data on ecological associations, particularly responses of population density to loss of elephants and clearance of woodland on sandy soils; protected in Kruger National Park, Leeuwfontein and Tswaing nature reserves (South Africa); Chobe National Park (Botswana).

Copris vrydaghi

Ferreira, 1962b



No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Estcourt (N.)' [Estcourt, KwaZulu-Natal, South Africa].
Taxonomy: Accepted Group 18 species, but often confused with close relatives; two female individuals from non-type localities require validation (N and S limits of range on map); sexually dimorphic (head and prothoracic disc), prominence of characters varies with body size.
Distribution: Moist grassland below central E escarpment: KwaZulu-Natal, South Africa.
Locality data (mean ± SD, range): Average altitude: 1 070 ± 183, 897–1 307 m; average annual rainfall: 758 ± 28, 729–794 mm; average annual temperature (max. + min. /2): 16.9 ± 1.4, 15.0–18.0°C (N=4).
Habitat: No quantitative assessment; not known.
Food types: No quantitative assessment; not known.
Temporal activity: Diel periodicity unknown, but possibly diurnal like its close relative, *C. caelatus* (Fabricius); active during the summer rainy season (Nov.).
Bioregions South Africa: Centred on Sub-Escarpment Grassland (Gs) (Grassland Biome).
Assessment rationale: EOO = 5 085 km^2 (probably underestimated); known by very few individuals in reference collections with some requiring validation; ecologically extremely poorly known, but appears to occupy a grassland range at lower altitude parallel to that of the central range of its close relative, *C. caelatus* (Fabricius, 1794); at present, would qualify for an IUCN threat category owing to small known range at few localities; however, paucity of data is likely a collection artefact, so currently assessed as Data Deficient (DD).
Conservation measures: To assess conservation status, a quantitative survey is required starting in the N Sub-Escarpment Grassland spreading to the S and to higher and lower altitude; this should determine the EOO, AOO, ecological associations and possible effects of habitat transformation; possibly protected at the iSandlwana Heritage Reserve (KwaZulu-Natal).

Genus *Heliocopris* Hope, 1837

Type species and designation: *Scarabaeus gigas* Linnaeus, 1758, by subsequent designation (Löbl 2006).
Synonyms: None.
Last review: Entire genus reviewed by Pokorný et al. (2009).

The long-established genus, *Heliocopris* Hope, 1837, was created to accommodate four previously described species. It is currently represented by 54 valid species occurring in the Afrotropical (50) and Oriental regions (4) with a fossil known from the Palaearctic region (Japan).

The genus is divided into five species groups (Pokorný et al. 2009), four of which are represented by seven species in South Africa, Botswana and Namibia. Validation is required concerning records for other species. In South Africa, records for *H. hamifer* Harold, 1878 may represent rare occurrence; records for *H. colossus* Bates, 1868, may represent past occurrence or misidentification of a rare close relative. In Namibia, records for *H. biimpressus* Kolbe, 1893b, may represent misdentification.

Heliocopris comprises very large-bodied species, whose nesting behaviour requires large amounts of dung. Even so, some taxa occur in dry or arid areas where large herbivores also occur. A relatively shallow tunnel is constructed from under a dropping into which dung is rapidly buried. In some species the dung is relocated into a deeper tunnel. A number of broods is constructed from the buried dung cake within a chamber at the end of the tunnel.

Heliocopris species are macropterous, flying during darkness. Three of the species are restricted to southern Africa whereas four species show distributions extending into tropical Africa. All are essentially centred on arid to moist savanna with three primarily recorded in the east on sandy or finer-grained soils. The others occur in both the east and the west with two rare or absent from the intervening Kalahari deep sands and two also present in the Kalahari. Despite their large body size, all species are assessed as Least Concern (LC) as they are widespread on farms and in reserves.

In southern Africa

Group 1 (*neptunus* group): One species centred on finer-grained soils in the east.
Group 2 (*hamadryas* group): Four mostly widespread species, three in east and west savanna with two also in the Kalahari, one primarily centred in the east.
Group 4 (*bucephalus* group): One species centred on finer-grained soils in the east.
Group 5 (*gigas* group): One widespread species associated with monogastric herbivore dung mostly in arid to dry savanna.

Heliocopris andersoni

Bates, 1868

= *Heliocopris isidis* Boheman, 1857
= *Heliocopris coriaceus* Shipp, 1897a

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'Prope Lacum N'Gami' [close to Lake Ngami, N Botswana]; *H. isidis*: 'Caffraria tota' [all southern/South Africa]; *H. coriaceus*: 'Amarato to Lake Stephanie' [untraced locality of 'Amarato' to Lake Chew Bahir, S Ethiopia].

Taxonomy: Accepted *gigas* group species; sexually dimorphic (head, prothoracic disc), prominence of characters varies with body size.

Distribution: Mostly dry savanna from S to NE Africa; South Africa, Namibia, Botswana, Zimbabwe, Kenya; also reported from Angola, Malawi, Mozambique, Democratic Republic of the Congo (DRC), Tanzania, Ethiopia, Eritrea.

Locality data (mean ± SD, range): Altitude: 1 057 ± 440 2–1 815 m; annual rainfall: 567 ± 192, 48–988 mm; annual temperature (max. + min. /2): 19.6 ± 2.0, 15.0–23.6°C (N=103).

Habitat: No quantitative assessment; DBRU collection records from sand (5), sandy loam (8), sandy clay loam (6), clay (1) in grassland (2), scrub/shrubland (4), open woodland (11).

Food types: No adequate quantitative assessment; at Phalaborwa: limited numbers sampled to dung of elephant (3) and pig (1), none to cattle (0); DBRU collection records from dung of elephant (5), rhinoceros (3), donkey (2), cattle (10), buffalo (1), wildebeest (1).

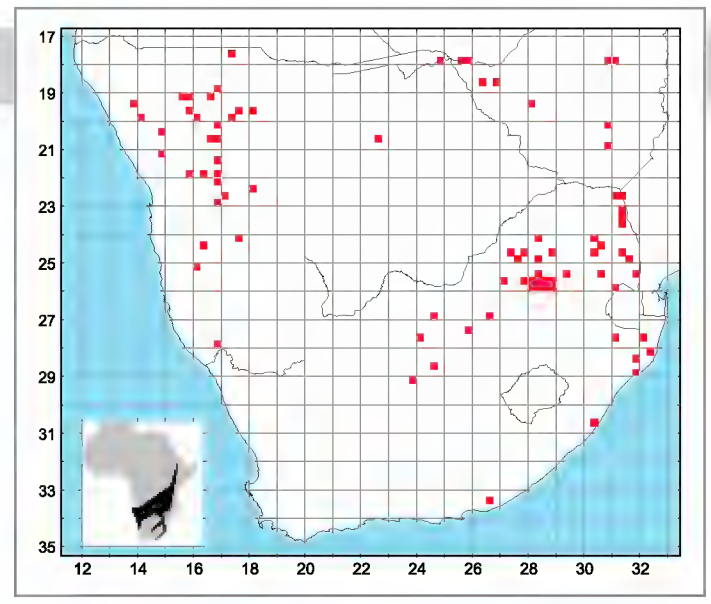
Temporal activity: Flight activity during darkness in the mid and late summer rainy seasons (Nov. to Apr.);

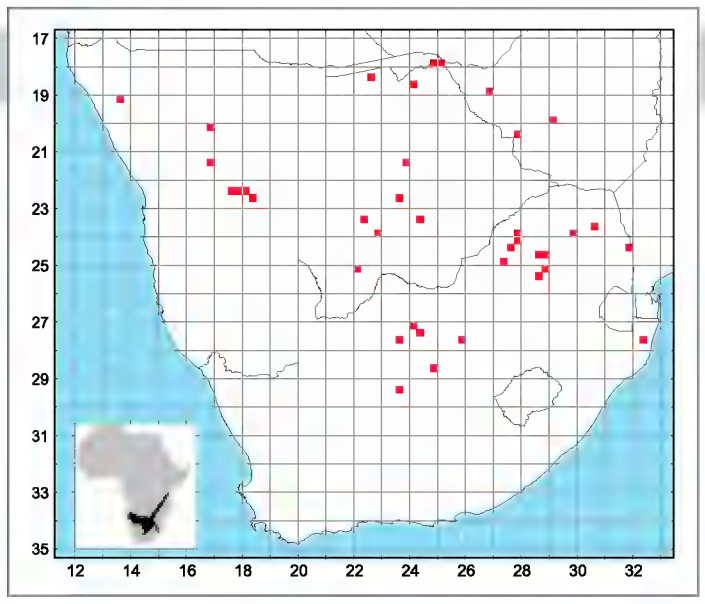
Ecoregions Namibia, Botswana, Zimbabwe: Mainly Namibian Savanna Woodlands (AT1316), Angolan Mopane Woodlands (AT0702), NE Kalahari Xeric Woodlands (AT1309), Zambezian and Mopane Woodlands (AT0725), Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Mainly Central Bushveld (SVcb), Lowveld (SVl), Mopane (SVmp) (Savanna Biome); also scattered in Eastern Kalahari Bushveld (SVk) (Savanna Biome), N Dry Highveld Grassland (Gh) (Grassland Biome); Albany Thicket Biome (AT).

Assessment rationale: EOO = 3 715 845 km² (gross estimate); limited data may point to association with monogastric herbivore dung although *H. andersoni* is widespread in both reserves and farmland; recorded primarily on monogastric herbivore dung in reserves, from cattle and equid dung on farms; assessed as Least Concern (LC) on basis of large range.

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, particularly better support for association with monogastric herbivore dung and effects on population density outside of reserves; protected in many game reserves and national parks including Kruger (South Africa), Etosha (Namibia), Lake Mutirikwe (Zimbabwe), Masai Mara (Kenya).





Heliocopris atropos

Boheman, 1860

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'prope lacum N'Gami' [close to Lake Ngami, N Botswana].
Taxonomy: Accepted *hamadryas* group species, but NE range edge uncertain due to possible confusion with close relatives in E Africa; sexually dimorphic (head, prothoracic disc), prominence of characters varies with body size.
Distribution: Dry Southern African savanna with a range that may extend to E Africa: South Africa, Namibia, Botswana, Zimbabwe, Angola; also reported from Malawi, Mozambique, Zambia; reports from Tanzania, Kenya require validation.
Locality data (mean ± SD, range): Altitude: 1 113 ± 323, 55–1 628 m; annual rainfall: 493 ± 149, 171–813 mm; annual temperature (max. + min. /2): 20.0 ± 1.7, 16.3–22.5°C (N=44).
Habitat: No adequate quantitative assessment; in open woodland of Leeuwfontein Nature Reserve: sand (3), sandy loam (5); DBRU collection records from sand (8), sandy loam (3) in grassland (5). open shrub/woodland (6).
Food types: No adequate quantitative assessment; on deep sands in Botswana: weak bias to monogastric herbivore dung: pig (1), elephant (7), cattle (1), sheep (1); DBRU collection records from dung of cattle (8), wildebeest (1), elephant (4).
Temporal activity: Flight activity in darkness during the summer rainy season (Nov. to May).
Ecoregions Namibia, Botswana, Zimbabwe: Primarily Kalahari Xeric Savanna (AT1309), Southern African Bushveld (AT0717), Zambezian and Mopane Woodlands (AT0725); also Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian Baikiaea Woodlands (AT0726).
Bioregions South Africa: Eastern Kalahari Bushveld (SVk), Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome).
Assessment rationale: EOO = 1 602 870 km^2 (gross estimate; range to E Africa?); AOO would be smaller if bias to sandy soils and monogastric herbivore dung is supported by quantitative data; however, large range across both farmland and reserves would justify an assessment as Least Concern (LC), although verging on Data Deficient (DD).
Conservation measures: Assessment of conservation status would be improved by more comprehensive quantitative data on ecological associations and a survey to more accurately determine NE range limits; protected in uMkhuze Game Reserve (South Africa), Chobe, Hwange and Bicuar national parks (Botswana, Zimbabwe, Angola).

Heliocopris faunus

Boheman, 1857

= *Heliocopris satyrus* Boheman, 1860
= *Heliocopris operosus* Waterhouse, 1891

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'prope fluvium Gariep' [close to Orange River, South Africa]; *H. satyrus*: 'prope lacum N'Gami' [close to Lake Ngami, N Botswana]; *H. operosus*: 'Africa'.

Taxonomy: Accepted *hamadryas* group species; sexually dimorphic (head, prothoracic disc); prominence of characters varies with body size.

Distribution: Somewhat patchy recorded pattern circumscribing the Kalahari to W, S and E: Namibia, E Botswana, S Zimbabwe, South Africa; unclear if this pattern is truly disjunct or a collecting artefact; higher population density on dry W uplands (N Namibian plateau, W escarpment edge) and South African Upper Karoo than in lower-lying E savanna where it occurs as a rarity; also reported from Mozambique; no recent Lake Ngami record (20.500S 22.667E), so not plotted on map.

Locality data (mean ± SD, range): Altitude: 1 177 ± 349, 55–1 928 m; annual rainfall: 376 ± 162, 103–900 mm; annual temperature (max. + min. /2): 18.4 ± 2.6, 13.3–23.0°C (N=69).

Habitat: No quantitative assessment; DBRU collection records from sand (4), sandy loam (5), sandy clay loam (2), clay (1) in pasture (1), scrub/shrubland (5), open woodland (6).

Food types: No quantitative assessment; DBRU collection records from dung of cattle (9), zebra (2).

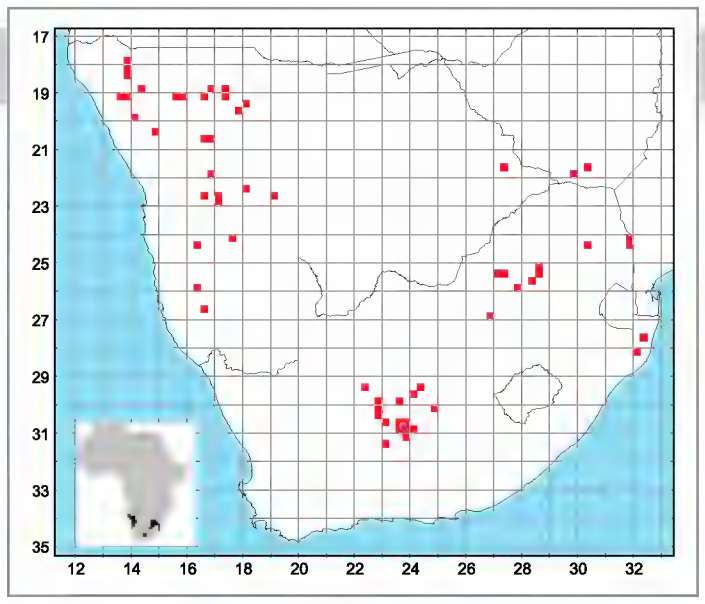
Temporal activity: Flight activity in darkness during the summer rainy season (Nov. to Apr.); attracted to light.

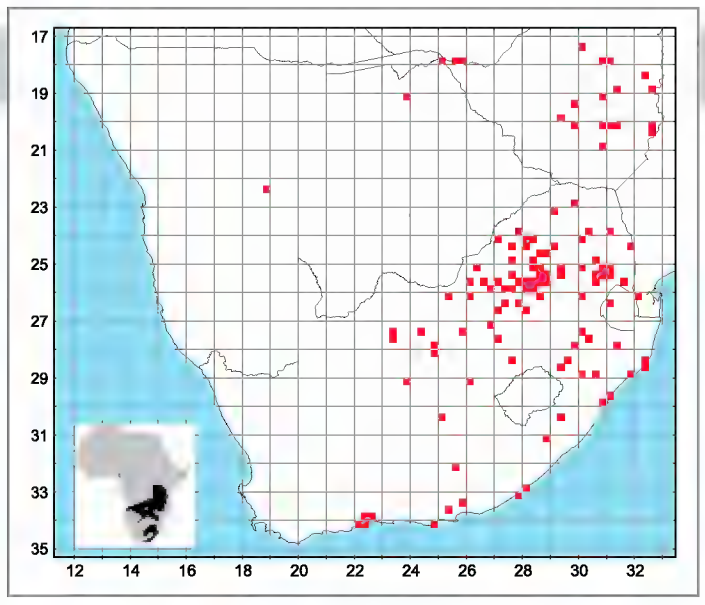
Ecoregions Namibia, Botswana, Zimbabwe: Mostly Namibian Savanna Woodlands (AT1316), NW Kalahari Xeric Woodlands (AT1309), Angolan Mopane Woodlands (AT0702); uncommon in Southern African Bushveld (AT0717), S Zambezian and Mopane Woodlands (AT0725).

Bioregions South Africa: Most records from Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome); Upper Karoo (NKu) (Nama Karoo Biome).

Assessment rationale: EOO = 391 450 km²; possible bias to sandy soils and low or open woody vegetation would reduce AOO; unclear if clearance of woody vegetation would influence population density; patchy, but widespread occurrence in farmland and reserves; readily attracted to cattle dung; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations and a survey to determine if patchiness is real or a collecting artefact; protected in Etosha National Park (Namibia).





Heliocopris hamadryas

(Fabricius, 1775)

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Scarabaeus hamadryas*: 'Cap. B. S.' [Cape of Good Hope, South Africa].

Taxonomy: Accepted *hamadryas* group species; sexually dimorphic (head, prothoracic disc); prominence of characters varies with body size.

Distribution: Primarily moist upland grassland and savanna in S, E and W central Africa, but also coastal in S Africa: South Africa: Zimbabwe, Malawi, Angola, Mozambique, Zambia, Kenya, SE Nigeria; outliers in Botswana, Namibia; also reported from Democratic Republic of the Congo (DRC), Rwanda, Tanzania, Uganda; records from Eritrea, Ethiopia, Somalia require validation.

Locality data (mean ± SD, range): Altitude: 1 068 ± 405, 0–1 800 m; annual rainfall: 678 ± 162, 326–1 232 mm; annual temperature (max. + min. /2): 18.6 ± 1.8, 13.7–23.0°C (N=155).

Habitat: In Gauteng bushveld: bias to deep sand (71) rather than sandy clay loam (14) and to shaded thickets (41) rather than open woodland (29), grassland (15); DBRU collection records across a wider range suggest soil generalisation: sand (9), sandy loam (9), sandy clay loam (11), clay (1) mainly in open vegetation: grassland/pasture (19), open shrub/woodland (4).

Food types: No quantitative assessment; DBRU collection records primarily from cattle dung (32), also elephant (1), rhinoceros (1).

Temporal activity: Flight activity in darkness during the summer rainy season (Nov. to May); attracted to light.

Ecoregions Namibia, Botswana, Zimbabwe: Primarily Southern Miombo Woodlands, also Zambezian and Mopane Woodlands (AT0725); marginal in two other ecoregions.

Bioregions South Africa: Dry Highveld Grassland (Gh), Sub-Escarpment Grassland (Gs) (Grassland Biome); Eastern Kalahari Bushveld (SVk), Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome); Indian Ocean Coastal Belt Biome (CB); transformed habitats of Albany Thicket and E Fynbos Biomes.

Assessment rationale: EOO = 3 416 220 km²; (gross, probable underestimate); AOO much smaller mostly coinciding with moist uplands and plateaux in the tropics; conflicting data for habitat associations, but widespread in reserves and farmland across a large range; readily attracted to cattle dung; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by further quantitative data on ecological associations, particularly an investigation to determine if vegetation bias to shade in Gauteng bushveld might reflect seasonal heat in summer activity period; protected in various reserves including Leeuwfontein (South Africa), Lake Mutirikwe (Zimbabwe), Masai Mara (Kenya).

Heliocopris japetus

Klug, 1855

= *Heliocopris bicarinulatus* Boheman, 1860

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Copris Japetus*: 'Sena' [Sena, Central Mozambique]; as *H. bicarinulata*: 'juxta lacum N'Gami' [near Lake Ngami, N Botswana].

Taxonomy: Accepted *hamadryas* group species; sexually dimorphic (head, prothoracic disc); prominence of characters varies with body size.

Distribution: Dry sandy savanna from S to E Africa: South Africa, Namibia, Botswana, Zimbabwe, Mozambique, Angola, Zambia, Kenya; also reported from Democratic Republic of the Congo (DRC), Tanzania; Rwanda and some DRC reports possibly represent confusion with close relative, *H. antenor* (Olivier, 1789).

Locality data (mean ± SD, range): Altitude: 1 020 ± 361 11–1 757 m; annual rainfall: 569 ± 178, 208–1 247 mm; annual temperature (max. + min. /2): 20.5 ± 1.7, 16.7–25.2°C (N=137).

Habitat: On Gauteng bushveld: extreme bias to deep sand (26) as opposed to sandy clay loam (0) with a slight bias to open woodland (14) as opposed to grassland (8) or shaded thickets (4); DBRU collection records support a bias to sand (23) as opposed to sandy loam (4), sandy clay loam (1), clay (2) in grassland/pasture (10), shrubland (3), open woodland (15).

Food types: On deep sand in Botswana: sampled only to dung with a bias to that of omnivores and monogastric herbivores: carrion (chicken livers – 0), dung of pig (28), elephant (27), cattle (11), sheep (10); DBRU collection records reflect commonly sampled dung types: cattle (29), elephant (5).

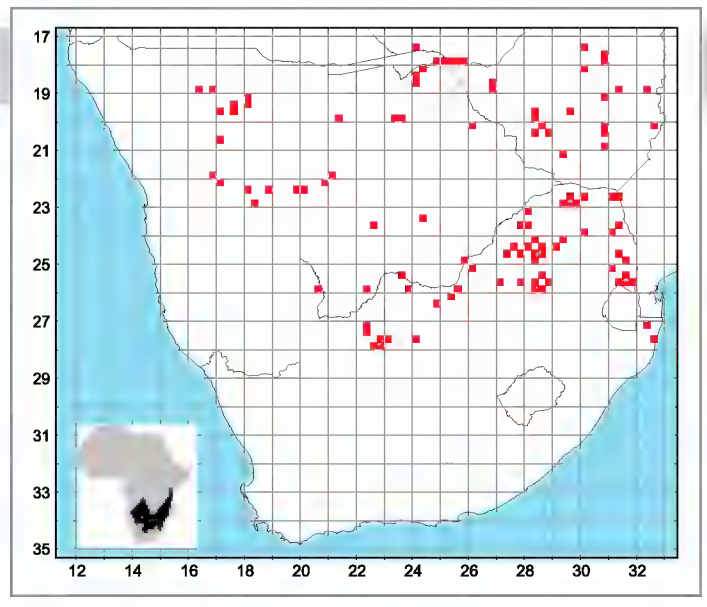
Temporal activity: Flight activity in darkness during the summer rainy season (Nov. to May); attracted to light.

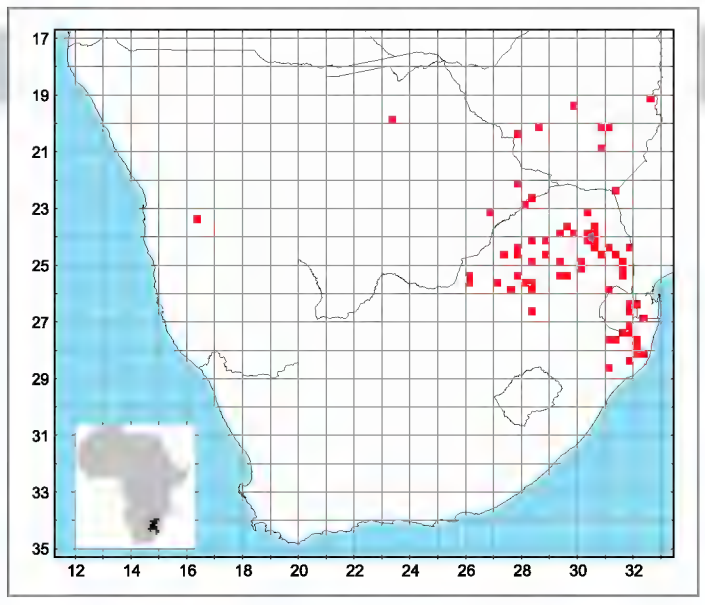
Ecoregions Namibia, Botswana, Zimbabwe: Kalahari Xeric Savanna (AT1309), Angolan Mopane Woodlands (AT0702), Southern African Bushveld (AT0717), Zambezian and Mopane Woodlands (AT0725), Southern Miombo Woodlands (AT0719), Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian Baikiaea Woodlands (AT0726); margins of two other ecoregions.

Bioregions South Africa: Eastern Kalahari Bushveld (SVk), Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome); margins of two other bioregions.

Assessment rationale: EOO = 3 260 895 km² (gross estimate); AOO would be restricted by sand specialisation; however, widespread in southern Africa where deep sands cover large areas; frequently recorded in both open and woody vegetation on farms and in reserves, especially at the fringes of the Kalahari; assessed as Least Concern (LC).

Conservation measures: None recommended; protected in various national parks, including Bicuar, Chobe, Hwange, Gorongosa, Kruger (respectively, Angola, Botswana, Zimbabwe, Mozambique, South Africa).





Heliocopris neptunus

Boheman, 1857

= *Heliocopris eryx* Fabricius, 1801, *sensu* Péringuey, 1901

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'juxta fluvium Limpopo' [near Limpopo River, southern Africa]; *H. eryx sensu* Péringuey: 'Transvaal (Lydenburg), Southern Rhodesia (Mazoe, Buluwayo)' [Mashishing, Mpumalanga, South Africa; Mazoe and Bulawayo, Zimbabwe].

Taxonomy: Accepted *neptunus* group species; sexually dimorphic (head, prothoracic disc); prominence of characters varies with body size.

Distribution: Moist southern African savanna: South Africa, Eswatini, NE Botswana, Zimbabwe, Mozambique; one outlier record in Namibia; also reported from Zambia; record from Ethiopia would represent confusion with a close relative.

Locality data (mean ± SD, range): Altitude: 824 ± 448, 46–1 746 m; annual rainfall: 653 ± 128, 229–1 013 mm; annual temperature (max. + min. /2): 19.9 ± 1.9, 14.0–24.5°C (N=83).

Habitat: No quantitative assessment; DBRU collection records only from finer-grained soils: sandy loam (4), sandy clay loam (3), clay (6) in grassland/pasture (4), open shrub/woodland (5).

Food types: No quantitative assessment; DBRU collection records entirely from cattle dung (15).

Temporal activity: Flight activity in darkness during the summer rainy season (Nov. to Apr.).

Ecoregions Namibia, Botswana, Zimbabwe: Southern African Bushveld (AT0717), S Zambezian and Mopane Woodlands (AT0725), Southern Miombo Woodlands (AT0719); scattered records in three other ecoregions.

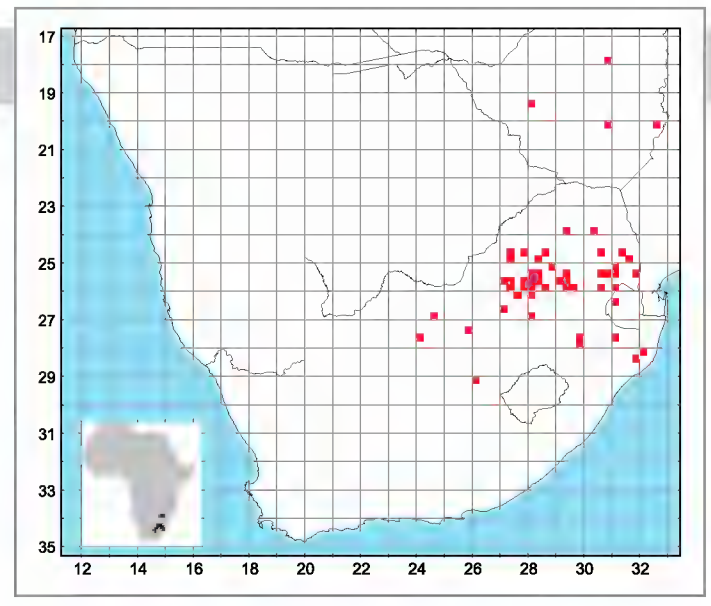
Bioregions South Africa: Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 328 720 km^2; (presumably underestimated); AOO would be restricted by soil specialisation, but requires quantitative support; however, finer-grained soils widespread in both reserves and farmland where it is readily attracted to cattle dung; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by a quantitative survey to confirm its full EOO, AOO and ecological associations; protected in Kruger National Park, Ithala Game Reserve (South Afrca).

Heliocopris pirmal

(Fabricius, 1798)



No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Copris pirmal*: 'India orientali' [ascribed to East India in error].

Taxonomy: Accepted *bucephalus* group species; identity of type requires validation; sexually dimorphic (head, prothoracic disc); prominence of characters varies with body size.

Distribution: Moist southern African savanna: South Africa, Eswatini, Zimbabwe; quite possibly Zambia; reports from Angola, Namibia, Botswana, Mozambique require validation; SW outlier localities require further support.

Locality data (mean ± SD, range): Altitude: 1 085 ± 362, 143–1 558 m; annual rainfall: 702 ± 113, 433–1 010 mm; annual temperature (max. + min. /2): 18.7 ± 1.6, 15.7–23.2°C (N=64).

Habitat: No quantitative assessment; very limited DBRU collection records from sandy clay loam (3) in grassland (1) or woodland (3).

Food types: No quantitative assessment; DBRU collection records from dung of cattle (1), buffalo (1), rhinoceros (4).

Temporal activity: Flight activity in darkness during the summer rainy season (Oct. to May); attracted to light.

Ecoregions Zimbabwe: Southern Miombo Woodlands (AT0719), Zambezian Baikiaea Woodlands (AT0726).

Bioregions South Africa: Particularly, moister parts of Central Bushveld (SVcb) and Lowveld (SVl) (Savanna Biome) along the Waterberg and edge of Highveld; scattered records in four other bioregions.

Assessment rationale: EOO = 236 025 km^2 (probably underestimated); AOO may be smaller due to finer-grained soil and woodland bias, but requires quantitative support; relatively poorly known species ecologically; assessed as Least Concern (LC) due to widespread distribution, but verging on Data Deficient (DD).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, particularly if population density might be influenced by clearance of woodland on finer-grained soils; improved survey data is also required to confirm its EOO and AOO; protected in Lake Mutirikwe Game Reserve (Zimbabwe), Hluhluwe–iMfolozi Game Reserve (South Africa).

Genus *Litocopris* Waterhouse, 1891

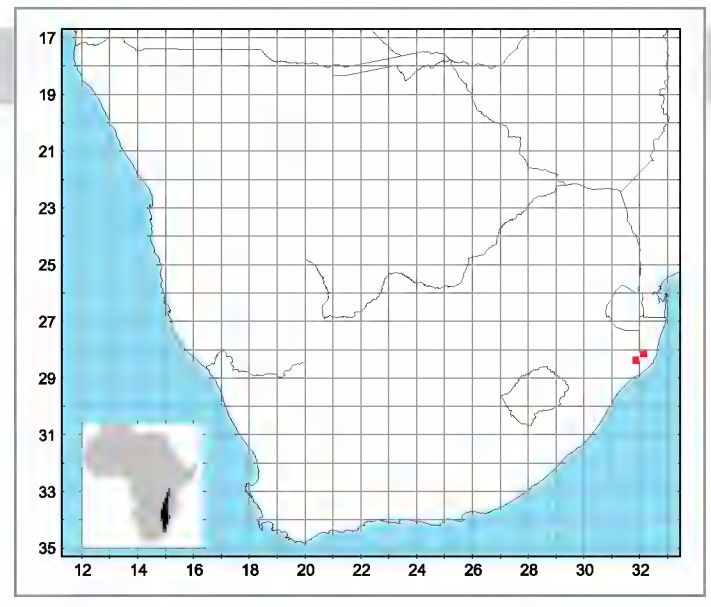
Type species and designation: *Litocopris punctiventris* Waterhouse, 1891, by subsequent designation (Ferreira 1960a).
Synonyms: None.
Last review: All species listed by Ferreira (1972).

Litocopris Waterhouse, 1891, was created as a subgenus of *Copris* to accommodate the type species and two others previously described under *Copris*. One further species was added at a later date. Although recently raised to generic level, this status has been questioned. After having being treated as a full genus (Branco 2011), it was synonymised with *Copris* (Marchisio & Zunino 2012), but has, thereafter, been listed as a genus by Catalogue of Life (Schoolmeesters 2017). Here we follow Branco (2011), although the taxon may show affinities to *Copris* Group 9, which is one of the more basally derived elements in the genus *Copris*.

Litocopris are macropterous with similar body size to the smaller-bodied group of *Copris*. They construct tunnels from under droppings, but nesting behaviour is essentially unknown. One species has often been observed in older dung. The two species represented in South Africa comprise an endemic centred on the SE coast and SE escarpment and another centred on moist savanna of NE KwaZulu-Natal, which is distributed northwards into the E tropics.

Litocopris muticus

(Boheman, 1857)



No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Copris mutica*: 'Caffraria interiori' [interior of SE South Africa].

Taxonomy: Accepted species, but see notes on generic status in genus section.

Distribution: Moist savanna on E seaboard of Africa: NE South Africa, Zimbabwe, Malawi, Mozambique, Kenya; also reported from Democratic Republic of the Congo (DRC), Rwanda, Burundi, Uganda, plus Côte d'Ivoire in W Africa.

Locality data (mean ± SD, range): Altitude: 257 ± 240, 59–808 m; annual rainfall: 912 ± 144, 697–1 177 mm; annual temperature (max. + min. /2): 22.2 ± 1.8, 20.5–25.2°C (N=11).

Habitat: No quantitative assessment; DBRU collection records biased to finer-grained soils: clay (3), sandy clay loam (3) sandy loam (2), sand (1); in shaded or partially shaded vegetation: forest (2), savanna woodland (10), grassland (1).

Food types: No quantitative assessment; DBRU collection records biased to monogastric herbivore dung: elephant (8), rhinoceros (4) with one record from human/cattle dung bait.

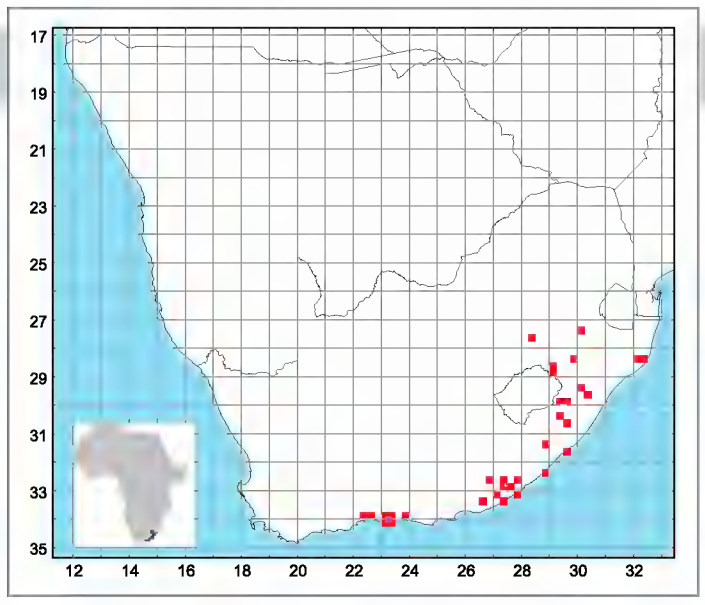
Temporal activity: Unknown; possibly flies during darkness, primarily during the summer rainy season (Oct. to May).

Ecoregions Zimbabwe: N Southern Miombo Woodlands (AT0719), wet areas in Zambezian and Mopane Woodlands (AT0725) (N Zimbabwe, not shown on map).

Bioregions South Africa: Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 793 435 km^2 (underestimated); AOO very likely much smaller as all DBRU collection records are from game reserves or protected areas (15); apparently somewhat specialised as regards soil, vegetation and dung type association, but assessed as Least Concern (LC) on the basis of widespread range in various reserves.

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, particularly as its status in South Africa would be dependent on continuing protection of both moist woodland vegetation on finer-grained soils and monogastric herbivores, particularly elephant and rhinoceros; protected in Hluhluwe–iMfolozi Game Reserve (South Africa), Gorongosa National Park (Mozambique), Masai Mara Game Reserve (Kenya).



Litocopris simplex

(Harold, 1868)

No synonyms

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Copris simplex*: 'Caffraria' [SE South Africa].
Taxonomy: Accepted species, but see notes on generic status in genus section.
Distribution: Moist SE Highveld and S to SE coastal regions of South Africa.
Locality data (mean ± SD, range): Altitude: 695 ± 625, 0–1 782 m; annual rainfall: 684 ± 164, 429–965 mm; annual temperature (max. + min. /2): 16.7 ± 2.1, 13.2–21.7°C (N=45).
Habitat: No quantitative assessment; DBRU collection records show a bias to finer-grained soils: clay (1), sandy clay loam (8), sandy loam (9); in grassland/pasture (14), shrub/woodland (2); also crop fields (2).
Food types: No quantitative assessment; all DBRU collection records from cattle dung (23).
Temporal activity: Unknown; possibly flies during darkness in the summer rainy season on the Highveld (Oct. to Mar.) with some activity in autumn and spring (Aug., Sept., May) along the warmer coastline.
Bioregions South Africa: SE Mesic Highveld Grassland (Gm) across Sub-Escarpment Grassland (Gs) to S outlier of Drakensberg Grasslands (Gd) (Grassland Biome); also Indian Ocean Coastal Belt Biome (CB) to NE margin of Albany Thicket Biome (AT); outlier cluster at W extreme of range coincides with high rainfall units of Sandstone Fynbos (FFs) or Southern Afrotemperate Forest (FOz 1).
Assessment rationale: EOO = 85 760 km^2; except for two woody localities at margins of Albany Thicket, DBRU records entirely from moist grassland or pasture on cattle dung whereas a number of non-DBRU records are from forest stations, pasture (3) or a fallow crop field (1); records for the outlier cluster in FFs and FOz 1 may merely infer tolerance of habitat modification, or it may infer range expansion into the Eastern Cape in response to clearance of shrubland and forest; nevertheless, currently assessed as Least Concern (LC) on the basis of widespread range.
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; particularly, a survey to examine habitat bias between forest and grassland in wet areas partly cleared of natural vegetation in the Eastern Cape; protected in Coleford Nature Reserve, but possibly poorly conserved over most of its range.

Genus *Macroderes* Westwood, 1842

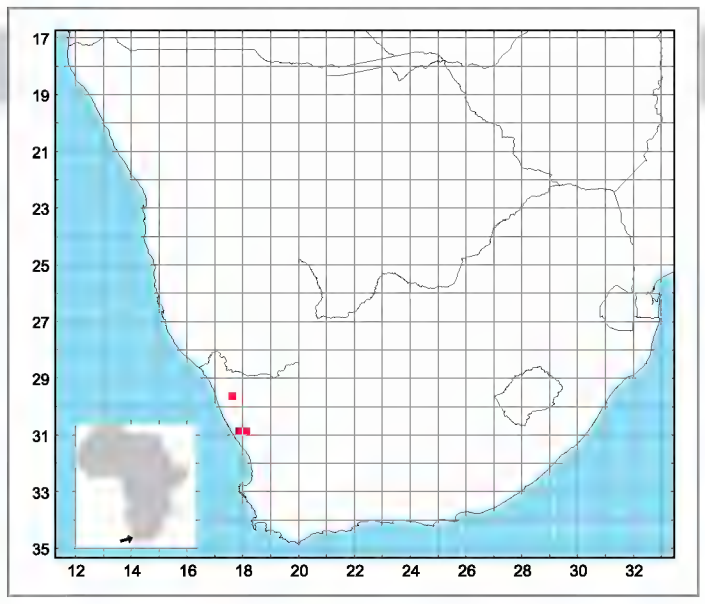
Type species and designation: *Onthophagus greeni* Kirby, 1818, by monotypy.
Synonyms: None.
Last review: Entire genus reviewed by Frolov and Scholtz (2004) and Abdalla et al. (2018) with synonymies and descriptions of new species.

The long-established genus, *Macroderes* Westwood, 1842, was created for a single species previously described under *Onthophagus*. After the revision of Frolov & Scholtz (2004), a total of 14 valid species was known with a further two names whose status could not be determined. More recent work has added a further seven new taxa and a further, now validated, old species name. Descriptions of these species were published too late to be included in the current species accounts, but see Preamble. *Macroderes* is endemic to the winter and bimodal rainfall regions of SW Africa where all but one species occupy relatively small, mostly allopatric ranges (Frolov & Scholtz 2004) in the winter rainfall region. Currently, all validated records occur entirely within the borders of South Africa.

Although there is no phylogeny (at the time of writing), morphological relationships between 13 species were indicated in the revision of Frolov and Scholtz (2004). These suggest four species groups showing E–W or N–S patterns of distribution. Two patterns extend along W coastal dunes comprising two and four species each. Another group of three species ranges from W to SE lowlands across the Cederberg. The remaining group of four species shows a disjunct pattern on cooler uplands with centres in Namaqualand, Cape Peninsula and the S Cape. Field observations suggest species-specific associations with either coarse or finer-grained soils.

All *Macroderes* species lack a humeral umbone, which is indicative of aptery and flightlessness and may account for the small species ranges. They are assumed to show tunnelling habits, but nesting behaviour is unknown. Some species have been sampled to dung-baited traps set in the late afternoon and retrieved the following morning. Although they were, thus, assumed to forage primarily in darkness, diurnal activity has been observed under particularly cold conditions. Thus, the dominant diel periodicity is uncertain.

Reference material and ecological information is comparatively limited, leading to assessments of Data Deficient (DD) for 12 species and Near Threatened (NT) for the remaining two. Observations made during field sampling suggest a bias to dense vegetation. Thus, habitat degradation, fragmentation and transformation would strongly influence conservation status, particularly considering their flightless condition. Overgrazing and mining are threats to species with N distributions although transformation is limited. Those in the more highly transformed SW and S would face greater threats. Irrespective of distributional bias, all but one species may deserve Vulnerable (VU) or even Endangered (EN) status on the basis of aptery and small known EOO averaging 2 325 km^2 and ranging from 53 to 7 940 km^2.



Macroderes amplior

Frolov & Scholtz, 2004

No synonyms

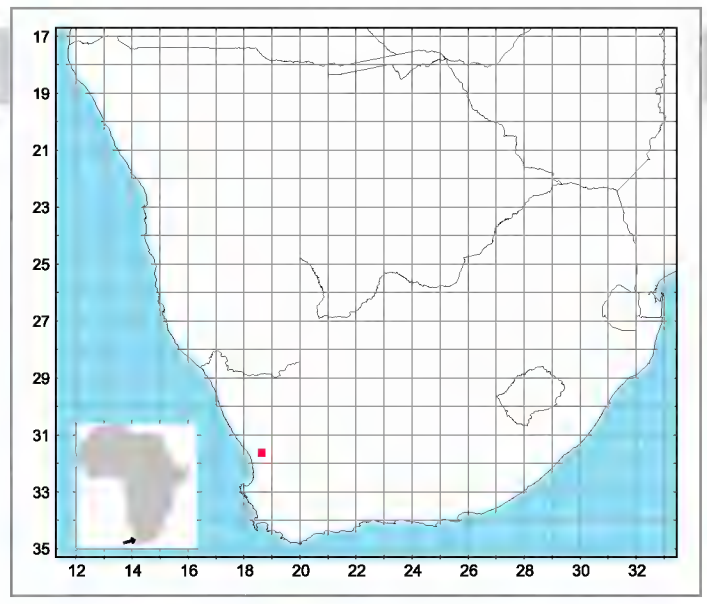
Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: '5 km W of Rietpoort' [Namaqualand, Northern Cape, South Africa].
Taxonomy: Accepted species.
Distribution: Lower edge, W escarpment, arid NW South Africa.
Locality data (mean ± SD, range): Altitude: 388 ± 85, 308–476 m; annual rainfall: 134 ± 27, 103–154 mm; annual temperature (max. + min. /2): 17.6 ± 0.6, 17.0–18.2°C (N=3).
Habitat: No quantitative assessment; one DBRU collection record from sandy loam in mountain Karoo shrubland.
Food types: No quantitative assessment; no recorded data.
Temporal activity: Flightless; diel periodicity uncertain; active during spring in the winter rainy season (Aug., Sept.), which may limit distribution to warmer, lower areas.
Bioregions South Africa: W Namaqualand Klipkoppe Shrubland (SKn 1) (Namaqualand Hardeveld Bioregion, Succulent Karoo Biome).
Assessment rationale: EOO = 1 170 km^2; known from only three localities in the SKn 1 vegetation unit where there is little habitat transformation as it is characterised by steep rocky habitats; however, although it covers about 9 900 km^2, much lies above 500 m and falls within the range of *M. mutilans* Kolbe, 1908; *M. amplior* is virtually unknown ecologically and is assessed as Data Deficient (DD), but, on the basis of flightlessness and very small known range, it would qualify for an IUCN threat category of at least Vulnerable (VU).
Conservation measures: To assess conservation status, a quantitative survey is required to determine the full EOO, AOO and ecological associations in SKn 1 and adjacent vegetation units; not currently known from any protected area.

Macroderes arrowi

Janssens, 1939a

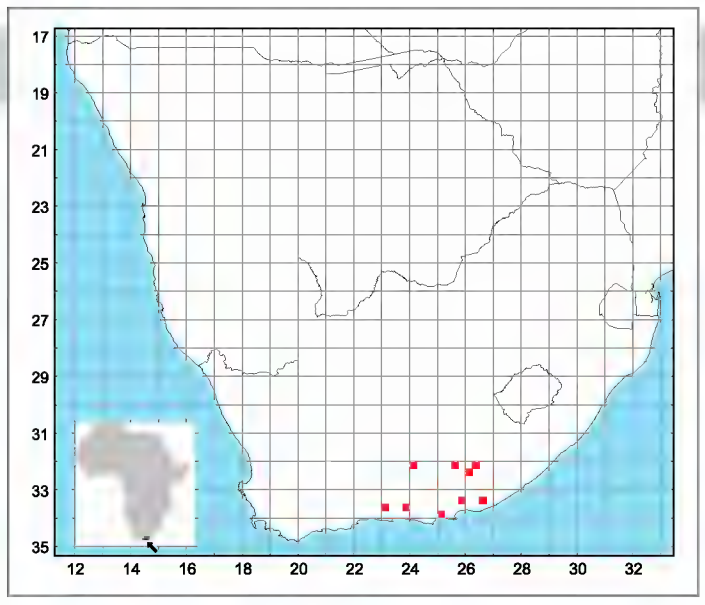


No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Rhynsdorp' [Vanrhynsdorp, Western Cape, South Africa].
Taxonomy: Accepted species.
Distribution: Recorded only on arid red sands in the vicinity of the type locality at Vanrhynsdorp, W coastal plain, South Africa.
Locality data (mean ± SD, range): Altitude: 218 ± 93, 152–283 m; annual rainfall: 161 ± 11, 153–169 mm; annual temperature (max. + min. /2): 18.7 ± 0.5, 18.4–19.1°C (N=2).
Habitat: No quantitative assessment; but one exact locality on deep red sands in scrub.
Food types: No quantitative assessment; no recorded data.
Temporal activity: Flightless; diel periodicity uncertain; active during spring in the winter rainy season (July to Sept.).
Bioregions South Africa: Red sands of Namaqualand Spinescent Grassland (SKs 12) (Namaqualand Sandveld Bioregion, Succulent Karoo Biome).
Assessment rationale: EOO = 52.5 km^2; currently known from only two localities with observations that suggest associations restricted to red sands of SKs 12 that cover a total of 521 km^2 in four natural patches; however, virtually unknown ecologically; assessed as Data Deficient (DD), but, on the basis of flightlessness and extremely small known range, it would qualify for an IUCN threat category of at least Vulnerable (VU), although little of SKs 12 has been transformed (4%).
Conservation measures: To assess conservation status, a quantitative survey of SKs 12 and adjacent vegetation units is required to determine the full EOO, AOO and precise ecological associations; not currently known from any protected area.



Macroderes bias

(Olivier, 1789)

= *Macroderes pilula* Sharp, 1880

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Scarabaeus bias*: 'Cap de Bonne-Espérance' [Cape of Good Hope, South Africa], neotype: 'Graham's Town' [Grahamstown, Eastern Cape, South Africa]; *M. pilula*: 'Grahamstown, Cap de Bonne-Espérance' [Grahamstown, Eastern Cape, South Africa].

Taxonomy: Accepted species.

Distribution: Dry, grassy to woody vegetation units in E bimodal rainfall region and edge of summer rainfall region, Eastern Cape, South Africa.

Locality data (mean ± SD, range): Altitude: 839 ± 458, 147–1 522 m; annual rainfall: 432 ± 77, 361–595 mm; annual temperature (max. + min. /2): 15.5 ± 2.0, 11.1–18.0°C (N=9).

Habitat: No quantitative assessment; one DBRU collection record from sandy loam in scrub; all but one of the known localities coincide with natural shrubland vegetation units.

Food types: No quantitative assessment; one DBRU collection record from cattle dung.

Temporal activity: Flightless; diel periodicity uncertain; active during spring, summer and autumn in the bimodal spring/autumn rainfall region (Sept. to May).

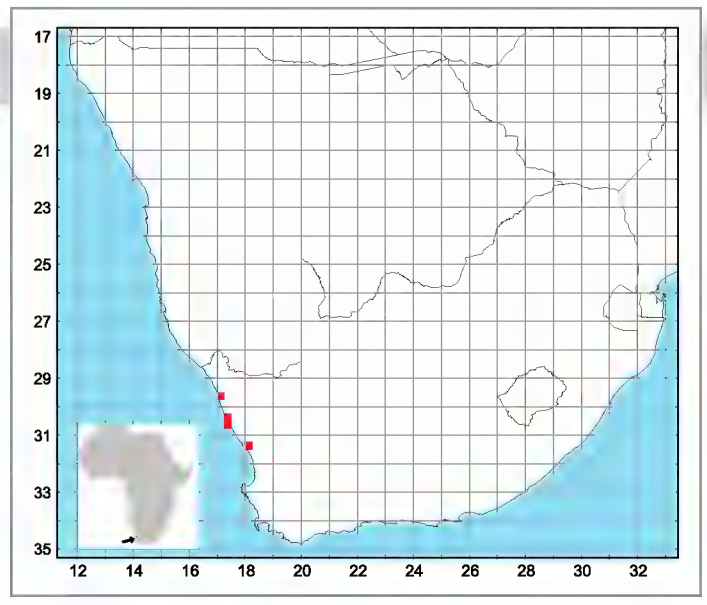
Bioregions South Africa: Vegetation units: In E Fynbos Biome: Shale Renosterveld (FRs 16), Sandstone Fynbos (FFs 28); in Albany Thicket Biome (AT 4, AT 6, AT 11); in Savanna Biome: Sub-Escarpment Savanna (SVs 7); in S Grassland Biome: wooded units of Sub-Escarpment Grassland (Gs 16, Gs 17), Dry Highveld Grassland (Gh 1).

Assessment rationale: EOO = 40 815 km^2; range across various grassy to woody vegetation units comparatively large; not known if AOO is influenced by soil and vegetation associations or habitat transformation, which is 2–20% in cited vegetation units; species little known, so assessed as Data Deficient (DD), but on basis of wide range, potentially Least Concern (LC) at present.

Conservation measures: To assess conservation status, quantitative data on ecological associations are required, particularly a comparison of population density data from grassy to more densely wooded vegetation units; protected in Addo Elephant National Park.

Macroderes cornutus

Frolov & Scholtz, 2004

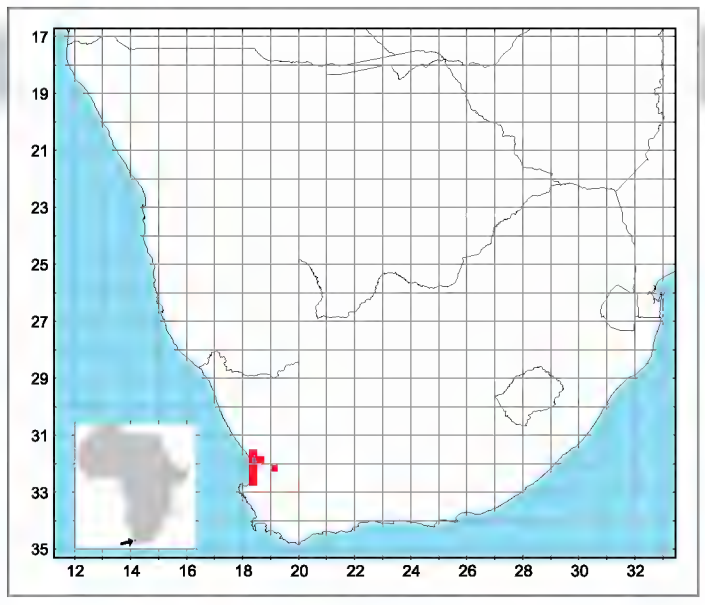


No synonyms

Global: DD (see IUCN Red List – DD)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Namaqualand, Sand Kop' [farm on W coast, South Africa].
Taxonomy: Accepted species.
Distribution: Arid deep W coastal sands, Namaqualand, Northern Cape, South Africa.
Locality data (mean ± SD, range): Altitude: 73 ± 54, 0–124 m; annual rainfall: 115 ± 33, 79–159 mm; annual temperature (max. + min. /2): 17.4 ± 1.0, 16.0–18.2°C (N=4).
Habitat: No quantitative assessment; all three known localities on deep sands supporting shrubland; two of the records from dunes.
Food types: No quantitative assessment; one record from a bush rat nest.
Temporal activity: Flightless; diel periodicity uncertain; active during spring in the winter rainy season (Aug., Sept.).
Bioregions South Africa: Namaqualand Coastal Duneveld (SKs 8), Namaqualand Strandveld (SKs 7) (Namaqualand Sandveld, Bioregion, Succulent Karoo Biome); also Namaqualand Sand Fynbos (FFd 1) (Sand Fynbos, Fynbos Biome).
Assessment rationale: EOO = 2 605 km^2; EOO presumably underestimated as SKs 7 and SKs 8 cover a combined area of ± 3 950 km^2 along the Namaqualand coast, some of which is protected in Namaqua National Park; FFd 1 covers ± 770 km^2; transformation 2–10%, especially by coastal mining and some inland cultivation, with extensive grazing pressure in SKs 7 and FFd 1; qualifies for an IUCN threat category of Vulnerable (VU) on the basis of small range and few known localities, but currently poorly known, so assessed as Data Deficient (DD).
Conservation measures: A quantitative survey of SKs 7, SKs 8 and FFd 1 is required to adequately assess conservation status; this needs to include assessment of ecological associations and effects of both habitat transformation and land usage; not currently recorded from any protected area.



Macroderes endroedyi

Frolov & Scholtz, 2004

No synonyms

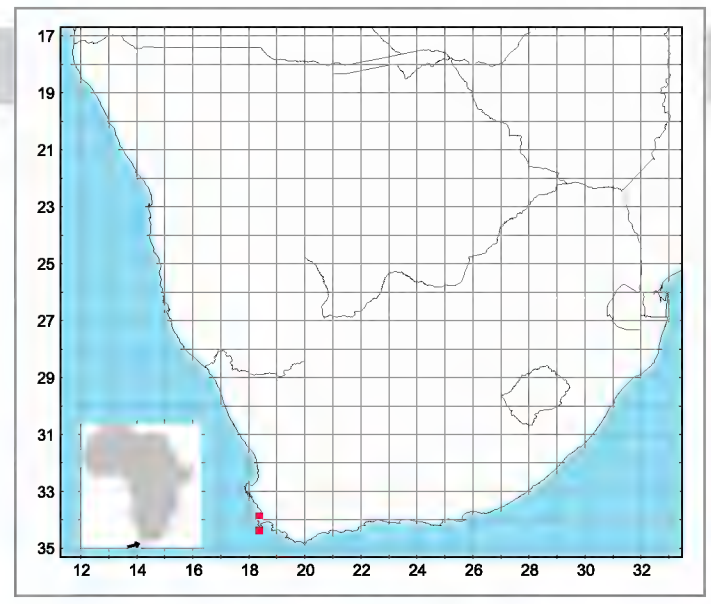
Global: NT (see IUCN Red List – NT)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'SW Cape, Nortier Farm' [W Coast, Western Cape, South Africa].
Taxonomy: Accepted species.
Distribution: Dry W coast deep sands, Western Cape, South Africa.
Locality data (mean ± SD, range): Altitude: 162 ± 102, 37–357 m; annual rainfall: 204 ± 28, 170–260 mm; annual temperature (max. + min. /2): 17.7 ± 0.5, 16.9–18.3°C (N=9).
Habitat: No quantitative assessment; no available data.
Food types: No quantitative assessment; sampled in ground traps baited with human dung and carrion.
Temporal activity: Flightless; diel periodicity uncertain; active during spring in the winter rainy season (Aug., Sept.).
Bioregions South Africa: Centred on deep sands of Lamberts Bay Strandveld (FS 1) (Western Strandveld, Fynbos Biome); also S tip Namaqualand Strandveld (SKs 7) (Namaqualand Sandveld Bioregion, Succulent Karoo Biome) plus NE edges of Graafwater Sandstone Fynbos (FFs 2), Cederberg Sandstone Fynbos (FFs 4) and Piketberg Sandstone Fynbos (FFs 6) (Sandstone Fynbos, Fynbos Biome).
Assessment rationale: EOO = 2 775 km^2; small range centred on FS 1, a deep sand and shrubland vegetation unit that has been 25% transformed by cultivation with additional pressures from long-term grazing; other records only at edges of some adjoining units; considering flightless habits and land utilisation pressures assessed as Near Threatened (NT) in line with the IUCN Red List although essentially Data Deficient (DD).
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, particularly responses to habitat transformation and grazing pressures; absence of records from Leipoldtville Sand Fynbos (FFd 2: 55% transformed) and presence at edges of adjoining Sandstone Fynbos vegetation units should be investigated as a possible habitat transformation effect; no current records known from protected areas.

Macroderes fornicatus

Sharp, 1880

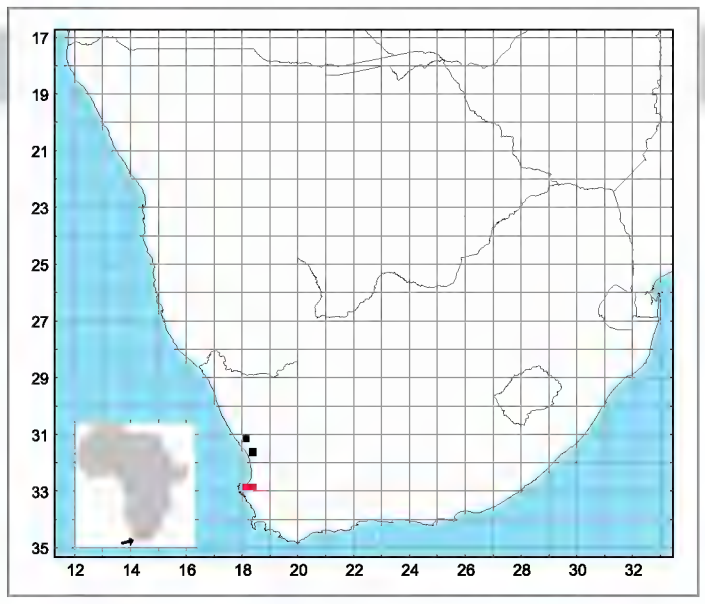


No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: Not stated.
Taxonomy: Accepted species.
Distribution: Currently known only from Cape Peninsula, SW Western Cape, South Africa.
Locality data (mean ± SD, range): Altitude: 235 ± 332, 0–469 m; annual rainfall: 454 ± 37, 428–480 mm; annual temperature (max. + min. /2): 15.2 ± 1.3, 14.3–16.2°C (N=2).
Habitat: No adequate quantitative assessment; on deep sands of Cape Peninsula: sampled only from dense low growth of *Restio*-dominated fynbos (burnt 2–3 yrs previously), not in open ericoid/proteoid fynbos (burnt 9–10 yrs previously) or in dense, low growth, Kikuyu pasture replacing natural shrubland (Farm Bonne Attente).
Food types: No quantitative assessment; sampled in low numbers to cattle dung (11).
Temporal activity: Flightless; diel periodicity uncertain; sampled from late winter to the end of spring in the winter rainy season (July to early Nov.).
Bioregions South Africa: Accurately mapped only to Peninsula Sandstone Fynbos (FFs 9) (Sandstone Fynbos, Fynbos Biome).
Assessment rationale: EOO = 535 km^2 (possibly underestimated); AOO possibly smaller as it is, currently, known only from FFs 9 covering ± 230 km^2 on the Cape Peninsula where it was localised to dense re-generating cover; although much is highly transformed (75%), most of the remainder is under protection; flightlessness and very small range in a highly exploited area would qualify for an IUCN threat category approaching Endangered (EN), however, currently assessed as Data Deficient (DD).
Conservation measures: Assessment of conservation status would be improved by a survey of Sandstone Fynbos in the vicinity of Cape Town, particularly lower-altitude parts of Kogelberg Sandstone Fynbos (FFs 11 – covering 888 km^2); further quantitative data on ecological associations are also required, particularly soil data and more detailed information on responses to vegetation cover; protected in Cape of Good Hope Nature Reserve, Cape Peninsula.



Macroderes foveatus

Frolov & Scholtz, 2004

No synonyms

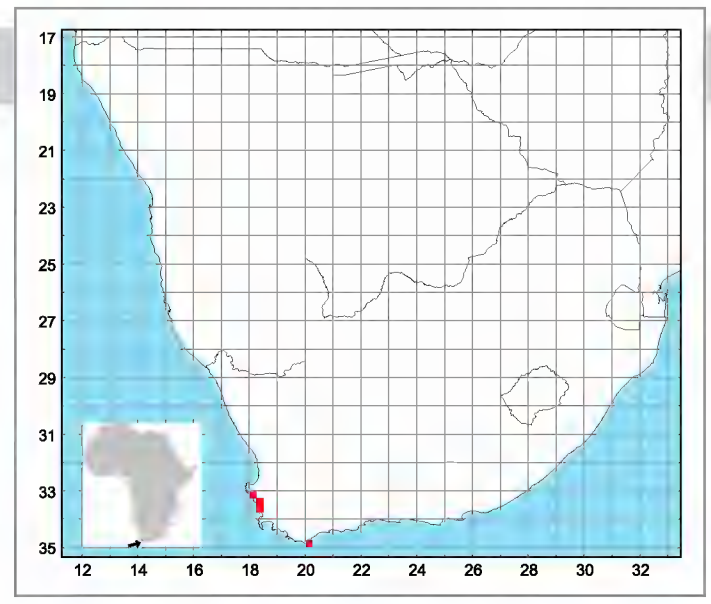
Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: '3 km E of Velddrif' [Western Cape, South Africa].
Taxonomy: Accepted species, but morphological differences at N localities (black squares), which fall within the range of the related *M. cornutus* Frolov & Scholtz, 2004; may equally be a further undescribed species.
Distribution: Restricted range in a shrubland vegetation unit on dry, deep, SW coastal sands, South Africa.
Locality data (mean ± SD, range): Altitude: 20 ± 25, 2–38 m; annual rainfall: 255 ± 16, 244–266 mm; annual temperature (max. + min. /2): 16.6 ± 0.1, 16.5–16.7°C (N=2 – red squares only).
Habitat: No quantitative assessment; no data available.
Food types: No quantitative assessment; sampled to human dung bait.
Temporal activity: Flightless; diel periodicity uncertain; active during spring in the winter rainy season (Aug.).
Bioregions South Africa: Hopefield Sand Fynbos (FFd 3) (Sand Fynbos, Fynbos Biome) (red squares only).
Assessment rationale: EOO = 105 km² (red squares only); type series recorded from two localities in a single vegetation unit that has been 40% transformed for arable farming and pasturage; on the basis of flightlessness and occurrence at few locations within an extremely small, threatened range, it would qualify for at least Vunerable (VU), even Endangered (EN), but currently assessed as Data Deficient (DD) due to absence of quantitative support.
Conservation measures: To assess conservation status taxonomic questions need to be resolved and a quantitative survey is required to determine EOO, AOO, ecological associations and whether clearance of natural shrubland influences population density or AOO; not currently known from any protected area.

Macroderes greeni

(Kirby, 1818)

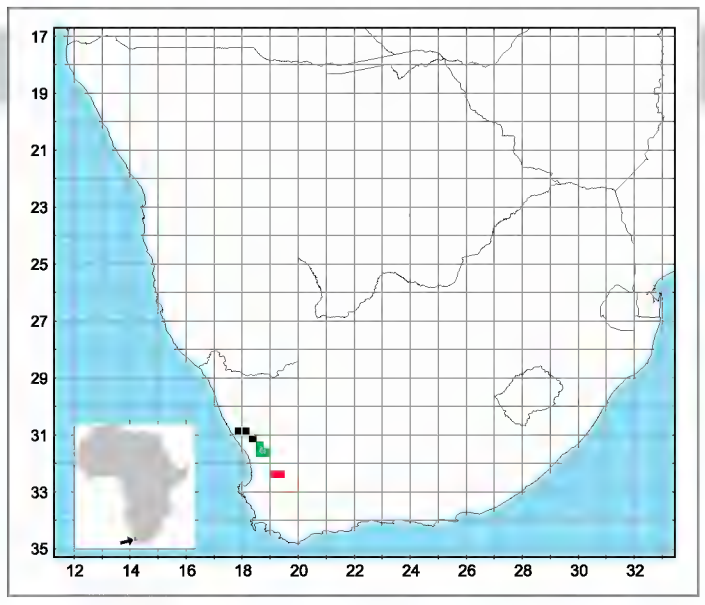


No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Onthophagus greeni*: 'Promontorium Bonae Spei' [Cape of Good Hope, South Africa].
Taxonomy: Accepted species.
Distribution: Dry coastal sands to N and SE of Cape Town, SW Western Cape, South Africa.
Locality data (mean ± SD, range): Altitude: 47 ± 41, 0–130 m; annual rainfall: 324 ± 50, 269–422 mm; annual temperature (max. + min. /2): 16.1 ± 0.5, 15.5–16.6°C (N=7).
Habitat: No adequate quantitative assessment; sampled on deep sand in open shrubland on farms Modderrivier (6), Pampoenvlei (2); also in shrubland at Geelbek (13), but not in adjacent sparse pasture cleared of natural shrubland (0).
Food types: No quantitative assessment; sampled to cattle dung.
Temporal activity: Flightless; diel periodicity uncertain; active in the winter rainy season; on SW coast: sampled primarily in autumn tailing off through winter to early spring (May to Sept.).
Bioregions South Africa: Langebaan Dune Strandveld (FS 5), Overberg Dune Strandveld (FS 7) (Western Strandveld); Atlantis Sand Fynbos (FFd 4) (Sand Fynbos, Fynbos Biome).
Assessment rationale: EOO = 1 535 km^2; presumably a deep sand specialist in natural shrubland although further quantitative support is required; occupies a small known range, part of which is highly transformed through cultivation and urban development (W coast: 35–40%, FS 5, FFd 4); it would qualify for an IUCN threat category of at least Vulnerable (VU) on the basis of flightlessness and small range in few locations, although currently assessed as Data Deficient (DD).
Conservation measures: Assessment of conservation status would be improved by a quantitative survey to determine full EOO, AOO, ecological associations and potential effects of habitat transformation; protected in Koeberg Nature Reserve and West Coast National Park where the sparse grassland on Geelbek has now been permitted to regenerate as natural shrubland.



Macroderes minutus

Frolov & Scholtz, 2004

No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'RSA, Western Cape Prov., 15 km SW of Lutzville' [South Africa] – [SW green squares on map].

Taxonomy: Currently an accepted species, but revision will probably reveal a complex of two or three species.

Distribution: Different members of species complex depicted in different colours; mountains (Cederberg) [red squares] and coastal hardeveld or sandveld [black or green squares], SW Western Cape, South Africa.

Locality data (mean ± SD, range): Black and green squares (lowlands): altitude: 257 ± 136, 77–404 m; annual rainfall: 155 ± 9, 145–169 mm; annual temperature (max. + min. /2): 18.4 ± 0.6, 17.6–19.2°C (N=6). Red squares (Cederberg): altitude: 1 144 ± 702, 563–1 924 m; annual rainfall: 256 ± 63, 198–322 mm; annual temperature (max. + min. /2): 14.1 ± 3.8, 9.9–17.3°C (N=3).

Habitat: No quantitative assessment; some from deep sands; otherwise no precise soil or vegetation data.

Food types: No quantitative assessment; records from carrion, plus human and reedbuck dung.

Temporal activity: All members of complex flightless; diel periodicity uncertain; active during spring in the winter rainy season (July to Sept.).

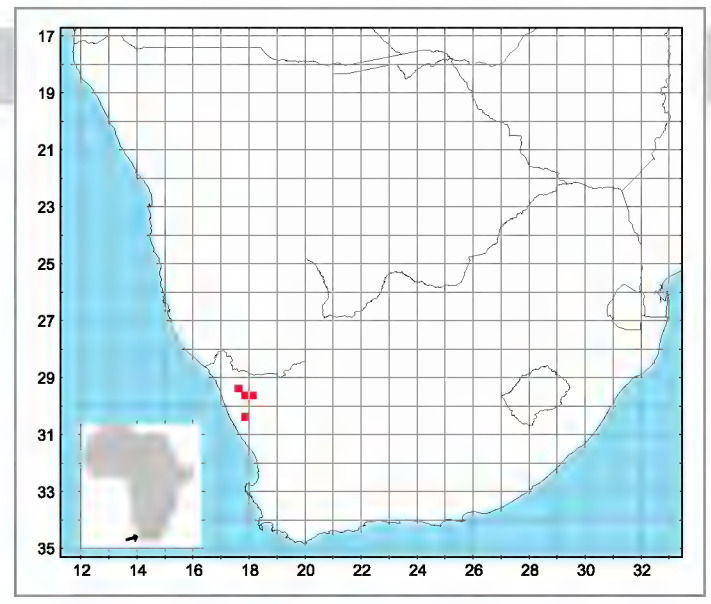
Bioregions South Africa: Vegetation units: black squares: Namaqualand Hardeveld (SKn 1) (Succulent Karoo Biome); green squares: Knersvlakte Quartz Vygieveld (SKk 3), Vanrhynsdorp Gannabosveld (SKk 5) (Succulent Karoo Biome), also Namaqualand Riviere (Azi 1) (Inland Azonal); red squares: Swartruggens Quartzite Fynbos (FFq 2); Cederberg Sandstone Fynbos (FFs 4) (Fynbos Biome).

Assessment rationale: EOO for species complex = 5 045 km^2, with 2–20% habitat transformation across the combined range; thus, EOO could be < 2 000 km^2 for each of three species and AOO even smaller; coupled with flightless habits, each would qualify for an IUCN threat category approaching Endangered (EN); however, considering the poor state of taxonomic, distributional and ecological knowledge, currently assessed as Data Deficient (DD).

Conservation measures: Conservation status may only be assessed once taxonomic revision has resolved issues of species identity and surveys have been conducted to determine full EOO, AOO, and ecological associations; Cederberg localities protected in Cederberg Wilderness Area; protection of taxa represented by green and black squares uncertain.

Macroderes mutilans

Kolbe, 1908

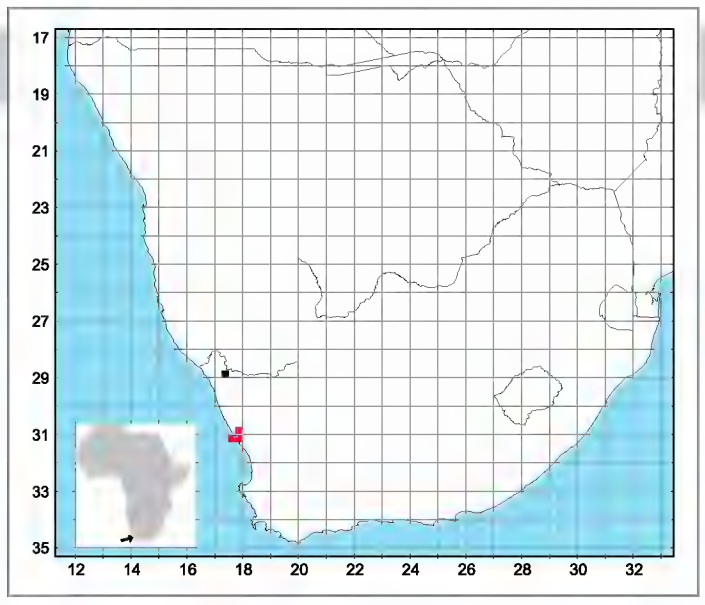


No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Klein Namaqualand : Steinkopf' [Steinkopf, Namaqualand, South Africa].
Taxonomy: Accepted species.
Distribution: Arid upper escarpment, Namaqualand, South Africa.
Locality data (mean ± SD, range): Altitude: 871 ± 98, 739–961 m; annual rainfall: 129 ± 27, 95–158 mm; annual temperature (max. + min. /2): 17.0 ± 0.8, 15.9–17.6°C (N=5).
Habitat: No quantitative assessment; no data available.
Food types: No quantitative assessment; no data available.
Temporal activity: Flightless; diel periodicity uncertain; active during late summer/autumn and spring in the winter rainy season; (Mar., Aug., Sept.).
Bioregions South Africa: Namaqualand Klipkoppe Shrubland (SKn 1), Namaqualand Blomveld (SKn 3) (Namaqualand Hardeveld Bioregion, Succulent Karoo Biome).
Assessment rationale: EOO = 1 501 km² (presumably underestimated); centred on a large upland area of arid scrub and shrubland on finer-grained soils; although SKn 1 is little transformed, SKn 3 is 6% transformed by cultivation and highly overgrazed; although the small known range and low number of localities would qualify for an IUCN threat category, currently assessed as Data Deficient (DD) pending survey of SKn 3 and the steep rocky hillsides of SKn1, which cover an area of ± 9 900 km², but also include the range of *M. amplior* Frolov & Scholtz 2004 on the lower escarpment to the W.
Conservation measures: Assessment of conservation status requires a quantitative survey to determine the full EOO, AOO, ecological associations, and particularly if overgrazing in SKn 3 is detrimental to population density or AOO; not currently recorded from any protected area.



Macroderes namakwanus

Frolov & Scholtz, 2004

No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Hoekbaai' [S Namaqualand, Western Cape, South Africa].
Taxonomy: Accepted species.
Distribution: Arid, W coastal deep sands on Western Cape / Northern Cape border, South Africa; identity of single female paratype from outlier locality in Richtersveld (black square) requires validation.
Locality data (mean ± SD, range): Altitude: 148 ± 205, 0–498 m; annual rainfall: 126 ± 31, 70–144 mm; annual temperature (max. + min. /2): 17.9 ± 0.4, 17.3–18.3°C (N=5).
Habitat: No quantitative assessment; two paratype localities on white sands found close to the coast, one from yellow sands found more inland.
Food types: No quantitative assessment; sampled to human dung bait.
Temporal activity: Flightless; diel periodicity uncertain; active during spring in the winter rainy season (Aug., Sept.).
Bioregions South Africa: Central Namaqualand Strandveld (SKs 7) (Namaqualand Sandveld Bioregion, Succulent Karoo Biome).
Assessment rationale: EOO = 53 km^2 (range for red squares only); validated range extremely small lying between coastal ranges of *M. cornutus* Frolov & Scholtz, 2004, to the N and close relative, *M. endroedyi* Frolov & Scholtz, 2004, to the S; area around type locality little transformed, but on the basis of extremely small EOO and records from few locations, would qualify for an IUCN threat category of at least Vulnerable (VU); however, in view of severely limited ecological and distributional data, currently assessed as Data Deficient (DD).
Conservation measures: Assessment of conservation status requires that questions on the identity of the Richtersveld paratype be resolved; a quantitative survey of the vegetation units around the type locality is required to establish the EOO, AOO and ecological associations; all validated localities are in unprotected areas.

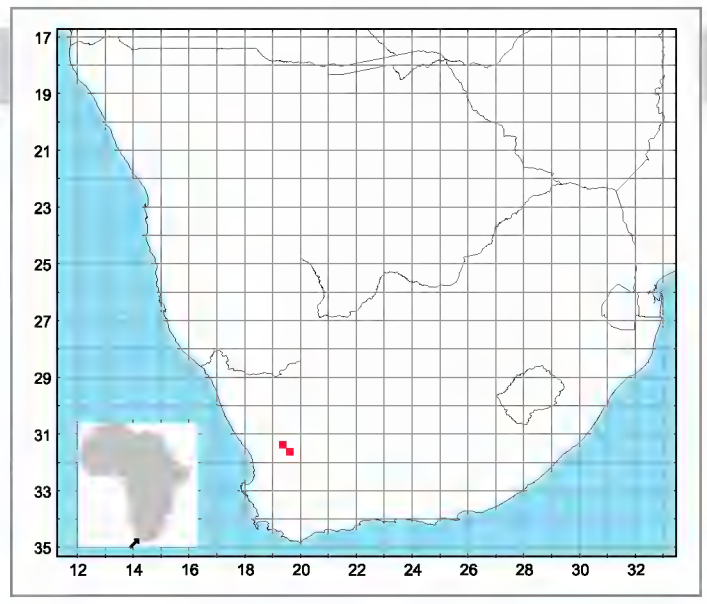
Macroderes nitidus

Harold, 1877b

No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: 'Cap bon. spei' [Cape of Good Hope, South Africa].

Taxonomy: Accepted species, but additional material from 'Cedarberg Range, east track' cited in the revision of Frolov and Scholtz (2004) is considered to belong to an undescribed species.

Distribution: Until recently known only from material bearing type labels comprising 12 individuals, six from an unstated spot locality in the Cape of Good Hope and six from 'Orlog Rivier' [Oorlogskloof River] that flows W from Calvinia; all collected by 'Meyer', a medical doctor who was based in that town; recently rediscovered after 156 years ± 40 km W of Calvinia.

Locality data (mean ± SD, range): Altitude: 791 ± 86, 730–851 m; annual rainfall: 169 ± 3, 167–171 mm; annual temperature (max. + min. /2): 17.0 ± 0.3, 16.8–17.3°C (N=2).

Habitat: No quantitative assessment; no data available.

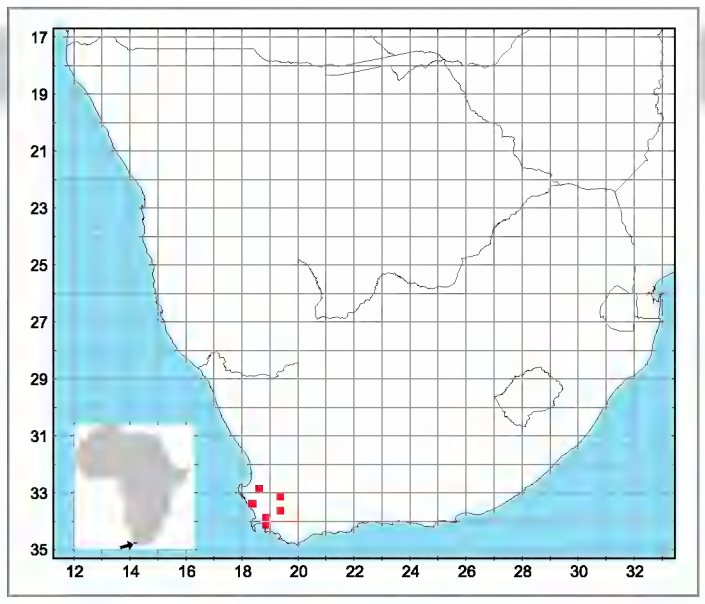
Food types: No quantitative assessment; no data available.

Temporal activity: Flightless; diel periodicity uncertain; active during spring in the winter rainy season (Aug.).

Bioregions South Africa: Vegetation unit: S Hantam Karoo (SKt 2) (Trans-Escarpment Succulent Karoo Bioregion, Succulent Karoo Biome).

Assessment rationale: EOO = 80 km^2 (underestimated); difficult to assess conservation status as there is only a single precise spot locality data and no ecological data; therefore, assessed as Data Deficient (DD); however, threats may be limited as SKt 2 covers a relatively large area (7 464 km^2) and is little transformed.

Conservation measures: To assess conservation status, a quantitative survey is required to determine the EOO, AOO and ecological associations; this survey should be focused on the area to the west of Calvinia and along the Oorlogskloof River in and around the SKt 2 vegetation unit; not currently known from any protected area.



Macroderes politulus

Preudhomme de Borre, 1880

No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Le patrie présumable est donc la Cafrerie' [presumably Caffraria, inexact locality in South Africa].
Taxonomy: Accepted species.
Distribution: Dry climate in Boland region of Western Cape, South Africa.
Locality data (mean ± SD, range): Altitude: 320 ± 245, 62–871 m; annual rainfall: 356 ± 76, 265–466 mm; annual temperature (max. + min. /2): 16.5 ± 0.7, 15.5–17.8°C (N=8).
Habitat: No quantitative assessment; one individual sampled over an entire year on sandy loam in grassland adjacent to a patch of degraded shrubland at farm Oranjefontein near Darling, Western Cape.
Food types: No quantitative assessment; one individual sampled to cattle dung.
Temporal activity: Flightless; diel periodicity uncertain; active during autumn, early winter and spring in the winter rainy season; (May to Oct.).
Bioregions South Africa: Various vegetation units centred around the Boland in the Fynbos Biome: Swartland Granite Renosterveld (Frg 2), Swartland Shale Renosterveld (Frs 9), Breede Alluvium Renosterveld (FRa 1), Lourensford Alluvium Fynbos (FFa 4), Winterhoek Sandstone Fynbos (FFs 5), Piketberg Sandstone Fynbos (FFs 6).
Assessment rationale: EOO = 7 940 km^2; small range centred in a region dominated by finer-grained soils and shrubland, much of which is highly transformed by agriculture or urban development (Frs 9: 90%; Frg 2: 80%; FFa 4: 90%; FRa 1: 57%); currently assessed as Data Deficient (DD) due to absence of quantitative data; although would deserve an IUCN threat category of at least Vulnerable (VU) on the basis of flightlessness and small, presumably fragmented range at few known locations; presence in mountain and lowland refuges is supported by an older record from the little-transformed FFs 5 (5%) and also several recent records (2006) from FFs 6 (17% transformed) and a patch of Renosterveld adjoining the sports field at Stellenbosch University.
Conservation measures: To assess conservation status, a quantitative survey is required to determine the full EOO, AOO and ecological associations; as removal of natural shrubland is likely detrimental to population density and AOO, a survey is required to determine the number of refuge locations occupied at the present time; not currently known from any protected area.

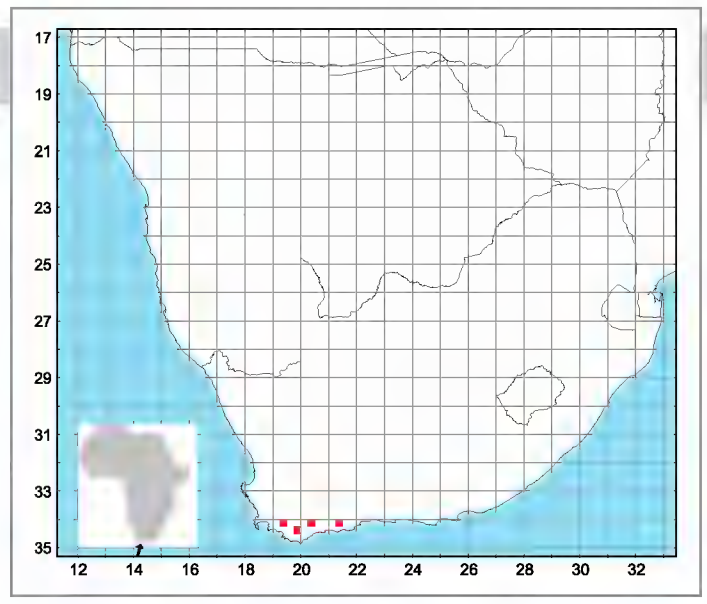
Macroderes undulatus

Preudhomme de Borre, 1880

= *Macroderes westwoodi* Preudhomme de Borre, 1880

Global: NT (See IUCN Red List – NT)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: *M. undulatus*: 'Cap de Bonne-Espérance'; *M. westwoodi*: 'Cap de Bonne-Espérance' [both Cape of Good Hope, South Africa].
Taxonomy: Accepted species.
Distribution: Mainly dry Renosterveld localities on low-lying S coastal hills, Western Cape, South Africa.
Locality data (mean ± SD, range): Altitude: 277 ± 179, 161–541 m; annual rainfall: 388 ± 21, 366–412 mm; annual temperature (max. + min. /2): 16.7 ± 0.6, 15.8–17.4°C (N=4).
Habitat: No quantitative assessment; limited DBRU collection records from a fallow crop field adjoining a patch of natural shrubland after July rainfall and from sandy clay loam in pasture resulting from clearance of natural shrubland.
Food types: No quantitative assessment; limited DBRU collection records from cattle dung (2).
Temporal activity: Flightless; diel periodicity uncertain; active during autumn and winter in the winter rainy season (May, July).
Bioregions South Africa: Various vegetation units in Fynbos Biome along S coastal hills: Western Rûens Shale Renosterveld (FRs 11), Central Rûens Shale Renosterveld (FRs 12), Eastern Rûens Shale Renosterveld (FRs 13); also Swellendam Silcrete Fynbos (FFc 1).
Assessment rationale: EOO = 2 300 km^2 (presumably underestimated); AOO perhaps restricted to finer-grained soils that once supported Renosterveld shrubland; because of the high level of transformation by cultivation (80–87%: FRs 11, FRs 12, FRs 13) and low numbers of records, assessed as Near Threatened (NT) to align with the IUCN Red List, although essentially Data Deficient (DD).
Conservation measures: Assessment of conservation status would be improved by a quantitative survey to establish the full EOO, AOO, ecological associations, and how population density or AOO might be influenced by the extreme habitat transformation, particularly in Rûens Renosterveld (± 5 870 km^2); this is required to justify the NT assessment; not currently known from any protected area although a few reserves occur within its range.

Genus *Metacatharsius* Montreuil, 1998

Type species and designation: *Scarabaeus ferrugineus* Olivier, 1789, by original designation.
Synonyms: None.
Last review: All species reviewed by Balthasar (1965b) with a few other species described subsequently (Balthasar 1968, 1970; Frey 1975a; Walter 1976).

Metacatharsius Paulian, 1939, was originally described as a subgenus to accommodate 16 species previously described under *Catharsius*. However, under international rules of nomenclature postdating 1930, the name was considered invalid as no type species was designated. A type species was only proposed by Montreuil (1998) together with a matrix of characters to separate the taxon from others at generic level. According to Branco (2011) this action satisfied international nomenclatural rules, so that Montreuil became the author of this taxon. However, this change from *Metacatharsius* Paulian, 1939, may be open to dispute.

There is no phylogeny and no division into species groups even though the genus comprises 64 species. Of these, 63 are restricted to the Afrotropical region and one is shared with the Palaearctic region in a Saharo–Sindian pattern of distribution. Although there are 16 currently valid names for South Africa, Botswana and Namibia, only 11 species accounts are presented. Arrangements of more than one species per account reflect suspected unpublished synonymies, indicating that taxonomic revision is required. No species account was prepared for one species, *Metacatharsius transvaalensis* Balthasar, 1968, as its identity could not be determined with confidence in comparison with a few other unnamed possibly undescribed species.

Metacatharsius species are much smaller-bodied than *Catharsius* species and, as such, would require less dung for breeding purposes. Tunnels are constructed from under droppings, but nesting behaviour has not been investigated. All species are macropterous showing flight activity in darkness. They may show a bias to carrion plus omnivore dung or a bias only to dung.

As association with sandy soils dominates the distributions of *Metacatharsius*, all but one southern African species show occurrence on deep Kalahari sands. The exception is centred on the arid southwest late summer rainfall region. Three other arid-centred species show distributions restricted to the southwest Kalahari (1), also radiating to the NW along the edge of the Namib Desert (1), or, with an additional, apparently disjunct occurrence, on the southwest coastal sands (1). Most other southern African species are centred in moister regions with distributions extending across most of the Kalahari to E outliers and the NE coastal sands of KwaZulu-Natal (5) with two known only from the NE Kalahari. Some of these patterns are dependent on the unpublished taxonomic interpretation used in the species accounts.

Because most distributions occur wholly or partly in relatively untransformed regions, taxa cited in eight of the species accounts are assessed as Least Concern (LC), whereas three are assessed as Data Deficient (DD) due to limited information or unresolved taxonomic problems. Additional taxonomic scrutiny is also required on three species pages where taxa are assessed as LC.

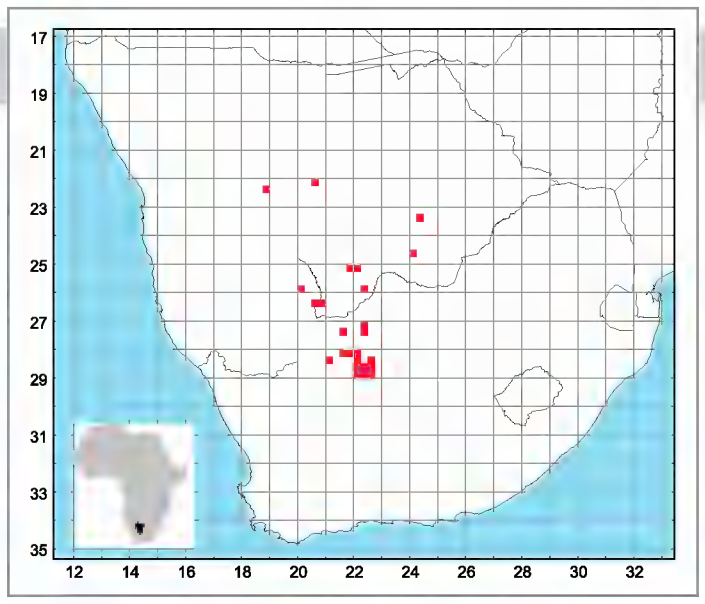
Metacatharsius anderseni

(Waterhouse, 1891)

= *Metacatharsius troglodytes* Boheman, 1857, *sensu* Pereira & d'Andretta, 1955
= *Catharsius* (*Metacatharsius*) *exiguiformis* Ferreira, 1964b (*pars*, 1 paratype)

Global: LC
Endemic: RSA, Botswana, Namibia

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: As *Catharsius anderseni*: 'Lake Nyassa' [=Lake Malawi, but would be an error; see notes on the Lake Ngami type locality of *Scarabaeus* (*Scarabaeolus*) *anderseni* Waterhouse, 1890]; *M. troglodytes sensu* Pereira & d'Andretta: Not stated; *C.* (*M.*) *exiguiformis pars*: 'Twee Rivieren' [Northern Cape, South Africa].

Taxonomy: Accepted species, but the synonymy of *M. troglodytes sensu* Pereira & d'Andretta, 1955, requires re-examination.

Distribution: Deep sands of the SW Kalahari: N South Africa, SW Botswana, E Namibia; recorded distribution in Mozambique is an error.

Locality data (mean ± SD, range): Altitude: 1 077 ± 113, 870–1 461 m; annual rainfall: 266 ± 50, 179–380 mm; annual temperature (max. + min. /2): 19.6 ± 0.6, 18.2–21.2°C (N=52).

Habitat: No adequate quantitative data; in Northern Cape: restricted to SW Kalahari (0.4/trap at 40 sampling sites), Upper Karoo (0), Bushmanland Karoo (0); few DBRU collection records: deep sand (2), grassland (1), open woodland (1).

Food types: On deep sands in SW Botswana (cited as *Metacatharsius* sp. A): only attracted to dung with distinct bias in association, sheep (144), cattle (8), elephant (32), pig (14), carrion (0); in Northern Cape: sampled to composite cattle/sheep dung baits.

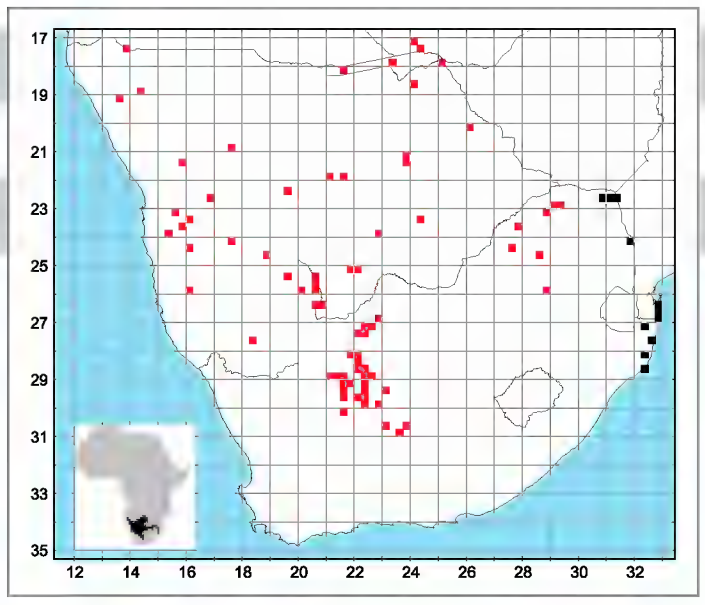
Temporal activity: Flight activity in darkness during the late summer rainy season (Jan. to Mar.).

Ecoregions Namibia, Botswana: Kalahari Xeric Savanna (AT1309).

Bioregions South Africa: Kalahari Duneveld (SVkd), E Eastern Kalahari Bushveld (SVk) (Savanna Biome).

Assessment rationale: EOO = 255 955 km^2; widespread on deep sands in a little-transformed area of grassland and open shrubland that is used primarily for the grazing of domestic livestock, particularly sheep, to whose dung this species is strongly attracted; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by further quantitative data on ecological associations; protected in Kgalagadi Transfrontier Park (South Africa, Botswana), Central Kalahari Game Reserve (Botswana).



M. dentinum

M. zuluanus

Metacatharsius dentinum

(Ferreira, 1964b)

Metacatharsius zuluanus

(Balthasar, 1965b)

No synonyms

Global: DD

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Catharsius* (*Metacatharsius*) *dentinum*: 'Sudoeste Africano: Matamata, Kalahari Gemsbok Park' [Mata Mata, South Africa]; As *Catharsius* (*Metacatharsius*) *zuluanus*: 'Südafrika, Zululand (Maputa)' [Manguzi, South Africa].

Taxonomy: Both currently accepted species, but *M. zuluanus* is possibly a junior synonym of *M. dentinum*; type series of both species need to be examined as possible synonyms of *M. pumilionis* (Wallengren, 1881) described from Christiana, NW Province, South Africa.

Distribution: Dry to moist savanna on deep sands of Kalahari, E Kalahari outliers, pre-Namib, E coastal plain: South Africa, Botwana, Namibia, S Mozambique, S Zambia; also reported from Angola.

Locality data (mean ± SD, range): *M. dentinum*: altitude: 1 034 ± 170, 388–1 809 m; annual rainfall: 294 ± 147, 56–710 mm; annual temperature (max. + min. /2): 19.5 ± 1.7, 15.5–23.4°C (N=114). *M. zuluanus*: altitude: 132 ± 185, 0–475 m; annual rainfall: 708 ± 166, 453–1 003 mm; annual temperature (max. + min. /2): 22.5 ± 0.6, 21.7–23.7°C (N=19).

Habitat: No quantitative assessment; limited DBRU collection records entirely on deep sand (5) in shrubland (5).

Food types: In Botswana: strong bias to carrion (chicken livers: 864), also attracted to dung, but much less abundant (pig: 151; elephant: 96; cattle: 88; sheep: 93); limited DBRU collection records on dead owl (2), rotten goat meat (1), dead millipede (1), cattle dung (1).

Temporal activity: Flight activity in darkness primarily during the summer rainy season (Sept. to May).

Ecoregions Namibia, Botswana, Mozambique: Primarily Namibian Savanna Woodlands (AT1316), Kalahari Xeric Savanna (AT1309), Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian Baikiaea Woodlands (AT0726), Maputaland Coastal Forest Mosaic (AT0119).

Bioregions South Africa: N Bushmanland (NKb), N Upper Karoo (NKu) (Nama Karoo Biome); Kalahari Duneveld (SVkd), Eastern Kalahari Bushveld (SVk), sand outliers in Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome); Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 1 111 720 km^2; all populations apparently deep sand specialists although quantitative support is required; populations currently named *M. dentinum* are widespread, largely in areas subject to low habitat transformation; they also show a strong bias to carrion association; despite apparent specialist attributes, both currently valid taxa deserve Least Concern (LC) status; however, they are assessed as Data Deficient (DD) owing to taxonomic uncertainty as they may comprise one or two species.

Conservation measures: Taxonomic issues need to be resolved before conservation status may be adequately assessed; quantitative data on ecological associations are also required, particularly the food associations of populations currently named *M. zuluanus*; protected in Kgalagadi Transfrontier Park (South Africa/Botswana), iSimangaliso Wetland Park (World Heritage Site) (South Africa).

Metacatharsius exiguiformis

(Ferreira, 1964b)

No synonyms

Global: LC
Endemic: RSA, Botswana, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Catharsius* (*Metacatharsius*) *exiguiformis*: 'Sudoeste Africano: Twee Rivieren' [Twee Rivieren, Northern Cape, South Africa].

Taxonomy: Accepted species, but SW Kalahari populations a little more shiny, usually with a more indented, less sinuous anterior clypeal margin.

Distribution: Centred on the SW Kalahari (red squares) and pre-Namib deep sands (black squares), arid late summer rainfall region: South Africa, Botswana, Namibia.

Locality data (mean ± SD, range): SW Kalahari: altitude: 1 064 ± 125, 802–1 461 m; annual rainfall: 263 ± 67, 142–453 mm; annual temperature (max. + min. /2): 19.7 ± 0.9, 17.9–21.4°C (N=146). Namib: altitude: 888 ± 392, 283–1 809 m; annual rainfall: 146 ± 114, 35–381 mm; annual temperature (max. + min. /2): 16.9 ± 1.0, 15.8–18.3°C (N=22).

Habitat: No quantitative assessment; DBRU collection records almost exclusively on deep sand (44), sandy loam (1) in grassland (11), scrub/shrubland (24), open woodland (8).

Food types: In Botswana: equally abundant on dung of pig (1 367), elephant (1 341) and sheep (1 436); much less abundant on cattle dung (390), uncommon on carrion (chicken livers: 29); however, DBRU collection records primarily from dung of cattle (34), also donkey (2), horse (1), wildebeest (1).

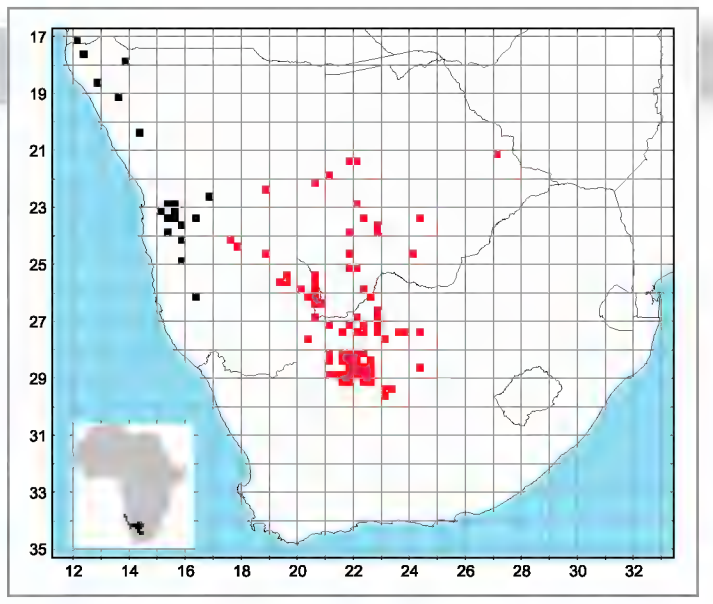
Temporal activity: Flight activity in darkness primarily during the late summer rainy season (Dec. to May).

Ecoregions Namibia, Botswana: Kalahari: SE Kalahari Xeric Savanna (AT1309); Namib: primarily straddling edges of Namibian Savanna Woodlands (AT1316), Namib Desert (AT1315), Kaokoveld Desert (AT1310).

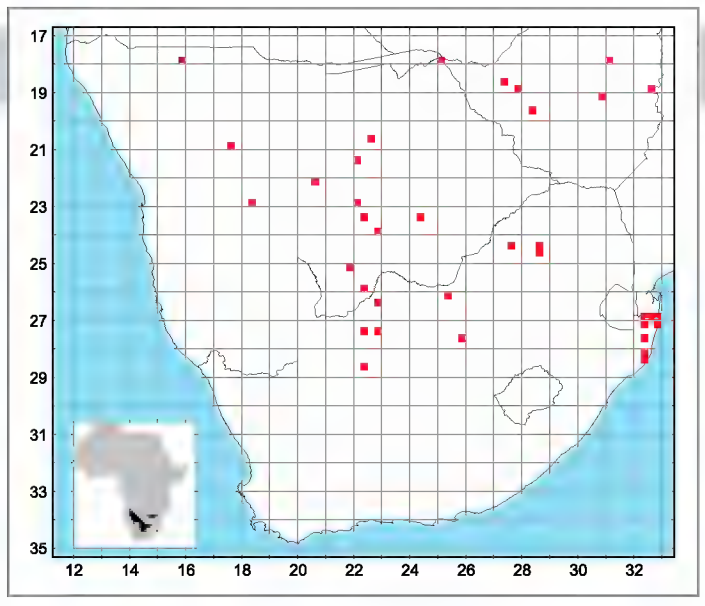
Bioregions South Africa: Kalahari Duneveld (SVkd), Eastern Kalahari Bushveld (SVk) (Savanna Biome); N extremities of Bushmanland (NKb) and Upper Karoo (Nama Karoo Biome).

Assessment rationale: EOO = 471 130 km^2; AOO would be smaller due to specialist association with deep sands, which are, nevertheless, extensive across its range; common in farmland of SW Kalahari and pre-Namib plains, which are used primarily for the grazing of domestic livestock, especially sheep; little habitat transformation; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on habitat associations; protected in Kgalagadi Transfrontier Park (South Africa/Botswana), Namib-Naukluft National Park (Namibia).



SW Kalahari



Metacatharsius exiguus

(Boheman, 1860)

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Copris exigua*: 'prope lacum N'Gami' [near Lake Ngami, N Botswana].

Taxonomy: Accepted species, but slight morphological variation between geographical centres; Kalahari and E outliers slightly indented clypeal margin; Zimbabwe and Angola less indented margin; Maputaland less indented more sinuous margin.

Distribution: Disjunct pattern in three dry to moist savanna centres of southern Africa related to soil type specialisation: South Africa, Botswana, Namibia, Angola, Zimbabwe; also reported from Mozambique.

Locality data (mean ± SD, range): Altitude: 827 ± 517, 0–1 503 m; annual rainfall: 557 ± 204, 278–971 mm; annual temperature (max. + min. /2): 20.7 ± 1.6, 17.6–23.1°C (N=40).

Habitat: No quantitative assessment; DBRU collection records primarily on deep sand (11), sandy loam (2) in grassland/pasture (6), shrubland (7), open woodland (3).

Food types: No quantitative assessment; DBRU collection records primarily from dung of cattle (15), also elephant (1).

Temporal activity: Flight activity in darkness primarily during the summer rainy season (Oct. to May).

Ecoregions Namibia, Botswana, Zimbabwe, Mozambique: Kalahari Xeric Savanna (AT1309), Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian Baikiaea Woodlands (AT0726), Southern Miombo Woodlands (AT0719), Maputaland Coastal Forest Mosaic (AT0119).

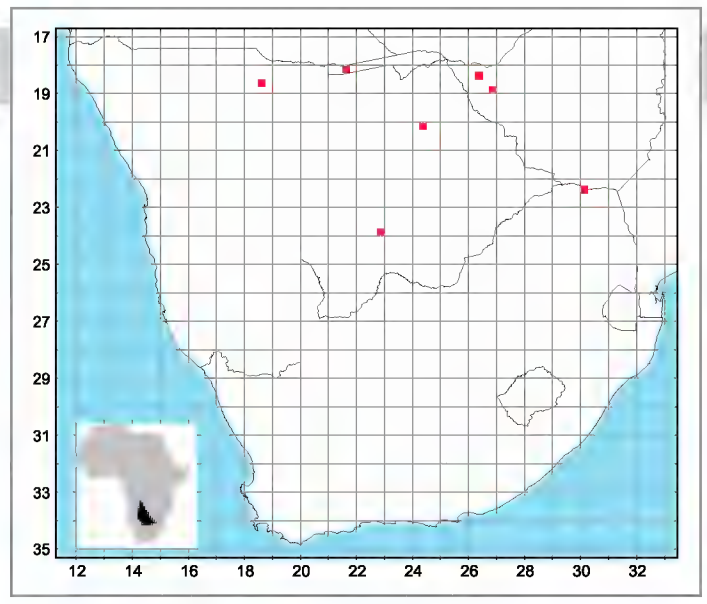
Bioregions South Africa: Deep sand patches in Savanna Biome: Eastern Kalahari Bushveld (SVk), Central Bushveld (SVcb), straddling SE border of Lowveld (SVl) into Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 680 625 km^2; AOO disjunct and smaller according to occurrence of deep sands, which are widespread in the SW Kalahari, Maputaland and parts of Zimbabwe; may also be restricted by occurrence of more open vegetation, but quantitative support required; habitat transformation low over SW part of range; assessed as Least Concern (LC) on basis of large EOO.

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; protected in Tswalu Kalahari Reserve, Tembe Elephant Park (South Africa).

Metacatharsius ferreirae

(Balthasar, 1965b)



= *Catharsius* (*Metacatharsius*) *dubius* Ferreira, 1962a
= *Catharsius* (*Metacatharsius*) *kochi* Ferreira, 1964b

Global: DD

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Catharsius* (*Metacatharsius) ferreirae*: *nom nov.* for *C.* (*M*). *dubius* [pre-occupied name] 'Camissombo, Calonda' [NE Angola]; *C.* (*M.*) *kochi*: 'Mangetti, entre Tsumkwe e Omassico' [NE Namibia].

Taxonomy: Accepted species; *M. kochi* is a synonym of *M. dubius*; as *Metacatharsius* was formerly considered a subgenus of *Catharsius*, *C.* (*M.*) *dubius* was a pre-occupied name (*Catharsius dubius* Péringuey, 1901); thus, it was provided with the *nom nov.* of *C.* (*M.*) *ferreirae*; types of *Metacatharsius rugosipennis* Frey, 1975, from 'Betchuanaland: Tsano' [?Tsane, Botswana] need to be compared as a likely junior synonym.

Distribution: Dry to moist savanna of N mega-Kalahari deep sands: South Africa, Zimbabwe, Botswana, Namibia, Angola.

Locality data (mean ± SD, range): Altitude: 951 ± 246, 499–1 196 m; annual rainfall: 459 ± 106, 341–608 mm; annual temperature (max. + min. /2): 22.0 ± 1.5, 20.0–24.3°C (N=8).

Habitat: No quantitative assessment; one DBRU collection record on deep sand in shrubland.

Food types: No quantitative assessment; one DBRU collection record on carrion (rotten goat meat).

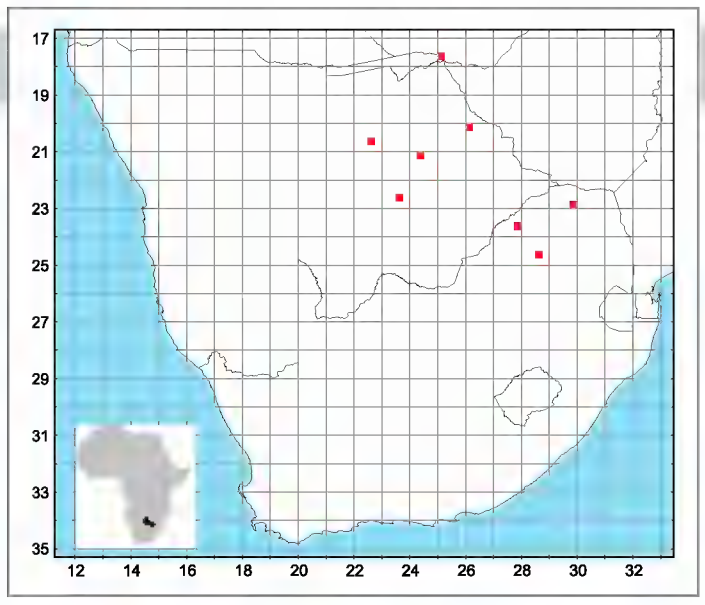
Temporal activity: Flight activity in darkness during the summer rainy season (Jan., Feb.).

Ecoregions Namibia, Botswana, Zimbabwe: Kalahari Xeric Savanna (AT1309), W Zambezian and Mopane Woodlands (AT0725), Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian Baikiaea Woodlands (AT0726).

Bioregions South Africa: Mopane (SVmp) (Savanna Biome).

Assessment rationale: EOO = 923 845 km^2; poorly known, but possibly a N mega-Kalahari deep sand and carrion specialist although quantitative data are required in support; currently assessed as Data Deficient (DD) although it is widely distributed across an area in which habitat transformation is comparatively low, overall.

Conservation measures: A survey is required to determine the full EOO and AOO; quantitative data on ecological associations are also required before it is possible to adequately assess conservation status; protected in Hwange National Park (Zimbabwe).



Metacatharsius freyi

(Ferreira, 1964b)

No synonyms*

Global: DD
Endemic: RSA, Botswana

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Catharsius* (*Metacatharsius*) *freyi*: 'Bechuanalândia: Ngami' [Lake Ngami, N Botswana].

Taxonomy: Accepted species, but validation required for species treated here as *M. freyi*, which was described from a single holotype male; *this holotype needs to be compared for synonymy with the type(s) of *M. pusio* (Kolbe, 1908) described as *Catharsius pusio* from 'Kalahari: Sekgoma-Khakea.....Khakea-Kang' [Sekumo to Kang, central Kalahari, Botswana].

Distribution: Dry to moist savanna on deep Kalahari sands and Kalahari outliers: N South Africa, Botswana; *M. pusio* cited from Botswana, Namibia.

Locality data (mean ± SD, range): Altitude: 994 ± 136, 817–1 222 m; annual rainfall: 512 ± 127, 354–684 mm; annual temperature (max. + min. /2): 20.8 ± 1.7, 17.9–22.7°C (N=10).

Habitat: No quantitative assessment; distribution coincides with continuous deep sands of the Botswana Kalahari and sand patches in E outliers.

Food types: No quantitative assessment; no data available.

Temporal activity: Like other *Metacatharsius* species, flight activity presumably in darkness during the summer rainy season (Oct. to Apr.).

Ecoregions Botswana: Primarily Kalahari Acacia-Baikiaea Woodlands (AT0709).

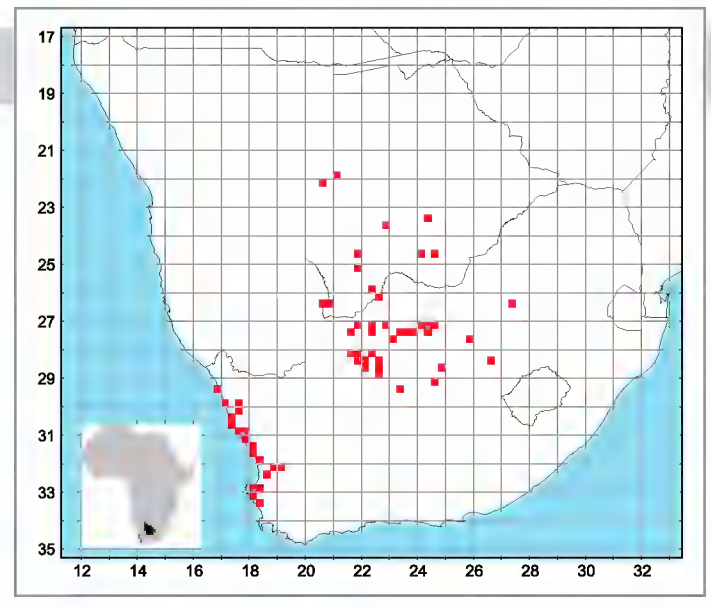
Bioregions South Africa: Sand patches in Central Bushveld (SVcb) (Savanna Biome).

Assessment rationale: EOO = 257 510 km^2 (presumably underestimated); widespread in N Botswana and N South Africa; probably a deep sand specialist and possibly primarily in wooded areas, but quantitative support required; possibility of threats due to clearance of woodland need to be investigated; currently assessed as Data Deficient (DD) due to poor state of knowledge both in terms of species identity and ecological associations.

Conservation measures: Taxonomic issues need to be resolved and quantitative data on ecological associations are required before an assessment may be made of conservation status; protected in Nylsvlei Nature Reserve (South Africa).

Metacatharsius latifrons

(Harold, 1868)



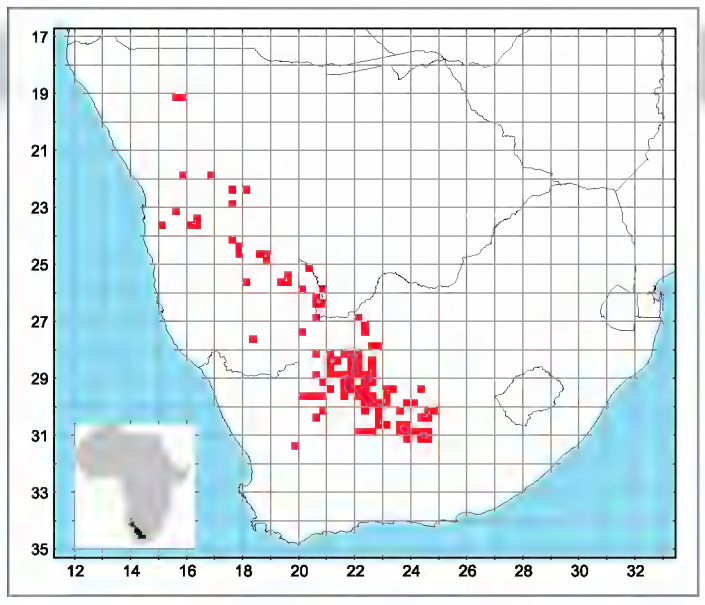
No synonyms

Global: LC
Endemic: RSA, Botswana

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Copris latifrons*: 'Cap bon. spei.' [Cape of Good Hope, South Africa].
Taxonomy: Accepted species.
Distribution: Arid deep sands: SW Kalahari (Namibia, Botswana, South Africa) and W coast, South Africa; uncertain if the disjunct pattern is real or a collection artefact; report from Mozambique is an error.
Locality data (mean ± SD, range): Altitude: 795 ± 517, 0–1 478 m; annual rainfall: 279 ± 112, 63–661 mm; annual temperature (max. + min. /2): 18.4 ± 1.3, 14.5–20.8°C (N=91).
Habitat: No quantitative assessment; DBRU collection records indicate a deep sand specialist: sand (39), sandy loam (3) in open vegetation: open woodland (4), scrub/shrubland (17), grassland (16); also fallow crop fields (2); in Northern Cape: entirely restricted to SW Kalahari (average of 0.08/sample at 23 study sites), none in Upper Karoo or Bushmanland Karoo.
Food types: No adequate quantitative assessment; in Botswana: sampled from pig (3), elephant (2) and sheep dung (2), not from cattle dung or carrion; DBRU collection records: dung of cattle (36), horse (1), donkey (1).
Temporal activity: Flight activity in darkness, primarily during the summer rainy season in the Kalahari (Oct. to Apr.); in the W coast winter rainfall region most records in spring (Sept.) but with activity continuing into the dry season (Sept. to Feb.).
Ecoregions Botswana: Kalahari Xeric Savanna (AT1309).
Bioregions South Africa: Centred on Kalahari Duneveld (SVkd), Eastern Kalahari Bushveld (SVk); Namaqualand Sandveld (SKs); Sand Fynbos (FFd), Western Strandveld (FS) (Biomes: Savanna – SV, Succulent Karoo – SK, Fynbos – F).
Assessment rationale: EOO = 322 620 km^2; widespread, but mostly recorded in low population density; however, much of range little transformed and used primarily for grazing of domestic livestock; transformation extensive only in extreme SW (25–70%) and E of range (13–42%) in South Africa; assessed as Least Concern (LC).
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; protected in West Coast and Namaqua national parks (South Africa), Kgalagadi Transfrontier Park (South Africa, Botswana) and Central Kalahari Game Reserve (Botswana).

5 mm



Metacatharsius marani

(Balthasar, 1940)

No synonyms

Global: LC
Endemic: RSA, Botswana, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Catharsius* (*Metacatharsius*) *mařani*: 'Süd-West Afrika, Okanjande und Karibib' [Namibia: Okanjande, Karibib].
Taxonomy: Accepted species.
Distribution: Centred on the arid late summer rainfall region: South Africa, SW extremity of Botswana, Namibia.
Locality data (mean ± SD, range): Altitude: 1 083 ± 199, 424–1 782 m; annual rainfall: 223 ± 62, 22–407 mm; annual temperature (max. + min. /2): 18.5 ± 1.8, 14.1–22.2°C (N=239).
Habitat: No adequate quantitative assessment; in Northern Cape: strong bias to arid Nama Karoo (Upper Karoo: 14.1; Bushmanland: 11.9) compared to dry SW Kalahari (2.8); DBRU collection records suggest a bias to sandy soils: sandy clay loam (3), sandy loam (5), sand (21) in open vegetation: open woodland (4), open scrub/shrubland (18), grassland (9).
Food types: No adequate quantitative assessment; at range edge in SW Botswana: attracted only to sheep dung (6), not dung of pig, elephant, cattle or to carrion (0); DBRU collection records from dung of cattle (18), wildebeest (1), horse (1), donkey (1), zebra (2).
Temporal activity: Flight activity in darkness during the late summer rainy season (Dec. to April), attracted to light.
Ecoregions Namibia: Centred on SW Kalahari Xeric Savanna (AT1309), Namibian Savanna Woodlands (AT1316); margins of two other ecoregions.
Bioregions South Africa: Centred on Upper Karoo (NKu), Bushmanland (NKb) (Nama Karoo Biome); marginal in Kalahari Duneveld (SVkd), E Eastern Kalahari Bushveld (SVk) (Savanna Biome).
Assessment rationale: EOO = 312 390 km^2; centred in a region that is little transformed and used primarily for the grazing of domestic livestock, particularly sheep; widespread and often abundant in farm rangeland; readily attracted to composite baits of cattle and sheep dung; assessed as Least Concern (LC).
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; protected in Kgalagadi Transfrontier Park (South Africa).

Metacatharsius opacus

(Waterhouse, 1891)

= *Catharsius cephalotes* Péringuey, 1892

Metacatharsius pseudoopacus

(Ferreira, 1965)

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Catharsius opacus*: 'Lake Ngami' [N Botswana]; *C. cephalotes*: Not stated; holotype as *Catharsius* (*Metacatharsius*) *pseudoopacus*: 'Província de Moçambique: Changalane' [S Mozambique].

Taxonomy: Currently both accepted species, but *M. pseudoopacus* considered to be a SE coastal synonym of *M. opacus*.

Distribution: Dry to moist savanna across N southern Africa and up E seaboard to E and NE Africa: South Africa, Eswatini, Botswana, Namibia, Angola, Zimbabwe, Zambia, Mozambique, Kenya, Somalia; also reported from Tanzania.

Locality data (mean ± SD, range): Altitude: 771 ± 432, 0–1 730 m; annual rainfall: 560 ± 189, 171–1 254 mm; annual temperature (max. + min. /2): 21.3 ± 1.7, 15.4–25.9°C (N=189).

Habitat: In uMkhuze Game Reserve: strong bias to deep sand (14.5), few on sand over clay (0.4), absent from sandy clay loam (0), clay (0); partly supported by DBRU collection records, bias to sand (35), but also sandy loam (13), sandy clay loam (2), primarily in wooded habitats, forest (6), open woodland (21), scrub/shrubland (13), grassland (4).

Food types: On deep sand in Botswana: relative food type generalist with slight bias to carrion (chicken livers: 313) and dung of pig (325), also dung of elephant (128), cattle (219), sheep (209); similar at Phalaborwa: dung of pig (65), elephant (35), cattle (22); DBRU collection records on dung of human/cattle or buffalo mix (7), elephant (7), rhinoceros (1), donkey (2), buffalo (1), cattle (43).

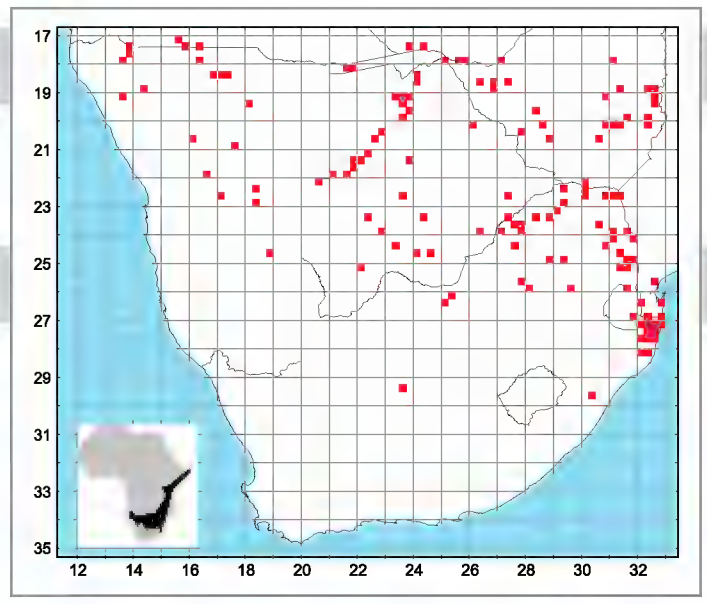
Temporal activity: Flight activity in darkness during the summer rainy season (Oct. to Apr.); attracted to light; at Phalaborwa: most active on warm evening soon after heavy rainfall (86), also cool evening after light rainfall (29), few on hot, dry evening (7).

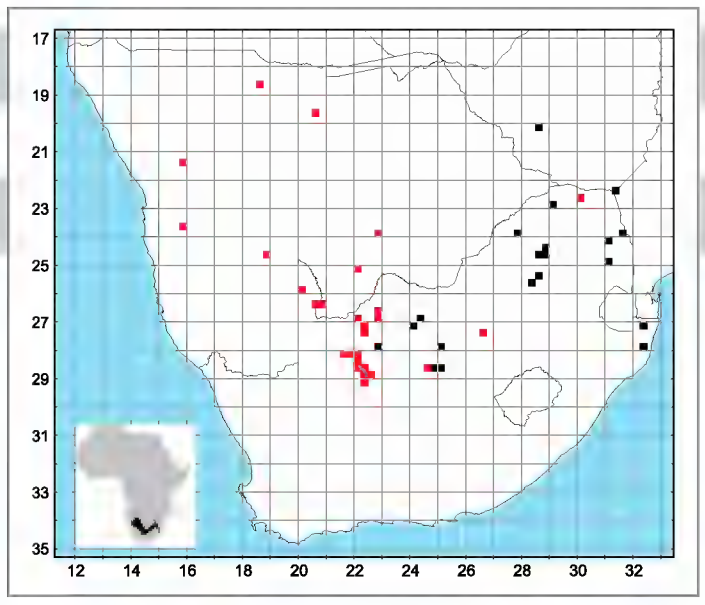
Ecoregions Namibia, Botswana, Zimbabwe, Mozambique: N Namibian Savanna Woodlands (AT1316), N Kalahari Xeric Savanna (AT1309), Angolan Mopane Woodlands (AT0702), Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian Baikiaea Woodlands (AT0726), Southern African Bushveld (AT0717), Zambezian and Mopane Woodlands (AT0725), Southern Miombo Woodlands (AT0719), Maputaland Coastal Forest Mosaic (AT0119).

Bioregions South Africa: Central Bushveld SVcb), Mopane (SVl), Lowveld (SVl) (Savanna Biome), N Indian Ocean Coastal Belt Biome (CB); scattered records in five other bioregions.

Assessment rationale: EOO = 3 129 685 km²; AOO probably smaller due to bias to coarser-grained soils and lower-altitude, woody vegetation; clearance of woodland would presumably reduce population density to very low levels; range in South Africa subject to variable degrees of habitat transformation (0–58%, SVl; 2–49%, SVcb; 0–20%, SVmp); however, very widely distributed and protected in various reserves; therefore, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by further quantitative data on habitat associations; in South Africa: protected in uMkhuze Game Reserve, Kruger National Park.





M. pumilionis

M. pumilioniformis

Metacatharsius pumilionis

(Wallengren, 1881)

Metacatharsius pumilioniformis

(Ferreira, 1964b)

No synonyms

Global: LC (for *M. pumilioniformis* – see IUCN Red List – LC)
Endemic: RSA, Botswana, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Copris pumilionis*: 'Ad Christianam semel lecta' [interpreted as collected at Christiana, NW Province, South Africa]; as *Catharsius* (*Metacatharsius*) *pumilioniformis*: 'Sudoeste Africano: Matamata' [Mata Mata, Northern Cape, South Africa].

Taxonomy: Both accepted species, but validation required in comparison with type(s) for species treated, here, as *M. pumilionis*, whose type(s) also need to be compared with those for *M. pumilioniformis* as W and E populations appear to be synonymous, although there are subtle differences; also see taxonomic notes for *M. dentinum* Ferreira, 1964b.

Distribution: *M. pumilionis* (black squares): dry to moist E savanna: South Africa, Zimbabwe; also cited from Botswana, Namibia; *M. pumilioniformis* (red squares): arid W savanna: South Africa, Botswana, Namibia; overlap at two squares in N Cape.

Locality data (mean ± SD, range): *M. pumilionis*: altitude: 949 ± 421, 60–1 395 m; annual rainfall: 523 ± 135, 328–853 mm; annual temperature (max. + min. /2): 19.7 ± 1.9, 17.3–24.5°C (N=25). *M. pumilioniformis*: altitude: 1 050 ± 132, 486–1 291 m; annual rainfall: 273 ± 83, 89–555 mm; annual temperature (max. + min. /2): 19.7 ± 1.1, 17.3–22.8°C (N=43).

Habitat: No adequate quantitative assessment; in a Northern Cape survey of the SW Kalahari and N Nama Karoo, *M. pumilioniformis* was restricted to the SW Kalahari, primarily on deep sands.

Food types: No adequate quantitative assessment; in Botswana: sampled in low numbers only to dung of cattle (5) and sheep (1), not to dung of pig, elephant or to carrion (chicken livers); occasionally sampled abundantly to sheep/cattle dung mixture in N Cape.

Temporal activity: Flight activity in darkness during the summer rainy season (Oct. to Apr.).

Ecoregions Namibia, Botswana, Zimbabwe: *M. pumilioniformis*: primarily Kalahari Xeric Savanna (AT1309). *M. pumilionis*: Southern African Bushveld (AT0717).

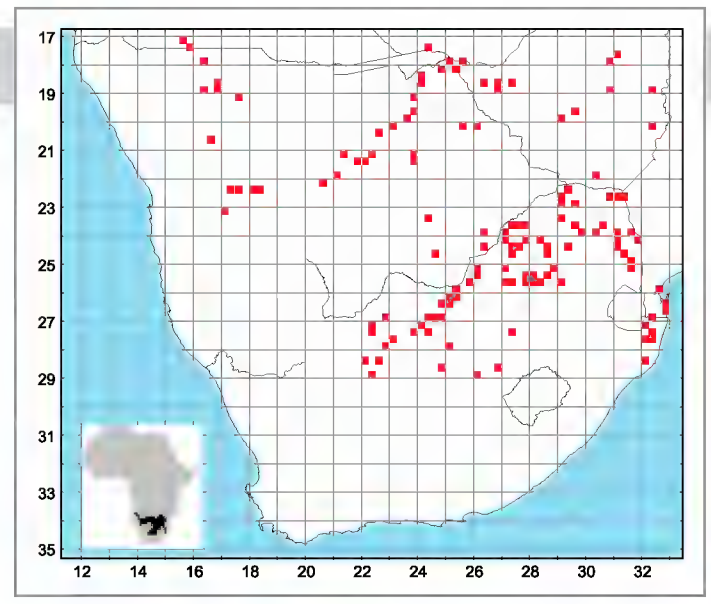
Bioregions South Africa: *M. pumilioniformis*: primarily Kalahari Duneveld (SVkd), Eastern Kalahari Bushveld (SVk). *M. pumilionis*: primarily Eastern Kalahari Bushveld (SVk), Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 688 900 km^2 (combined); AOO possibly smaller, restricted to deep sands, possibly in more open vegetation, but quantitative support required; *M. pumilioniformis* may be locally abundant in the N Cape (33.0 per sample) and may show a bias to ruminant herbivore dung; difficult to assess threat levels given poor state of taxonomic and ecological knowledge, but both assessed as Least Concern (LC) on basis of wide EOO of both populations sets on areas of deep sands.

Conservation measures: Taxonomic issues need to be resolved and quantitative data on ecological associations are required to improve the assessment of conservation status; *M. pumilioniformis* protected in Kgalagadi Transfrontier Park (South Africa / Botswana), *M. pumilionis* in Kruger National Park (South Africa).

Metacatharsius troglodytes

(Boheman, 1857)



No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Catharsius troglodytes*: 'juxta fluvium Gariep' [near Orange River, South Africa].

Taxonomy: Accepted species.

Distribution: Widespread in southern African savanna; mostly on moister deep sands of the Kalahari, its E outliers, and the SE coastal plain: South Africa, Mozambique, Zimbabwe, Botswana, Namibia, S Angola.

Locality data (mean ± SD, range): Altitude: 934 ± 408, 0–1 874 m; annual rainfall: 538 ± 148, 238–972 mm; annual temperature (max. + min. /2): 20.6 ± 1.8, 16.2–23.7°C (N=173).

Habitat: In Botswana: strong bias to moister NE (1656) compared to arid SW (156); in Gauteng bushveld: extreme bias to deep sand (129) compared to sandy clay loam (0) and to grassland (118) compared to open woodland (10) or shaded thicket (1); similar bias in uMkhuze Game Reserve: deep sand (16.3), sand on clay (1.5), sandy clay loam (0.0), clay (0.0) with 90% in grassland; only partly supported by DBRU collection records: deep sand (49), sandy loam (21), sandy clay loam (3) in grassland/pasture (14), scrub/shrubland (17), open woodland (37), shaded thicket (1).

Food types: In Botswana: attracted primarily to dung (pig: 446, elephant: 631, cattle: 206, sheep: 504) with few to carrion (chicken livers: 25); somewhat similar at Phalaborwa: pig (51), elephant (16), cattle (49); DBRU collection records from various dung types: cattle (57), wildebeest (1), waterbuck (1), elephant (9), donkey (1), human/cattle mix (1).

Temporal activity: Flight activity in darkness during the summer rainy season (Oct. to Apr.); in Gauteng: active from early summer (Oct.) rising to mid-summer peak (Dec.) tailing off to late summer (Mar.); at Phalaborwa: much greater activity on a warm evening soon after heavy rainfall (66) than on an evening following a hot, dry day (25) or an evening following a warm, cloudy day and light rainfall (23); attracted to light.

Ecoregions Namibia, Botswana, Zimbabwe, Mozambique: NW Kalahari Xeric Savanna (AT1309), Angolan Mopane Woodlands (AT0702), Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian Baikiaea Woodlands (AT0726), Zambezian and Mopane Woodlands (AT0725), Southern Miombo Woodlands (AT0719), Maputaland Coastal Forest Mosaic (AT0119).

Bioregions South Africa: Eastern Kalahari Bushveld (SVk), Central Bushveld (SVcb), Lowveld (SVl), Mopane (SVmp) (Savanna Biome); few records in Dry Highveld Grassland (Gh) (Grassland Biome).

Assessment rationale: EOO = 1 228 465 km^2 (estimated); AOO would be smaller owing to soil type specialisation, but deep sands and species range are widespread in southern Africa; bias to open vegetation suggested by quantitative data so probably not influenced adversely by clearance of woodland; also readily attracted to various dung types including that of farm livestock; assessed as Least Concern (LC).

Conservation measures: None recommended at the present time; protected in Kruger National Park, uMkhuze Game Reserve (South Africa), Chobe National Park (Botswana).

Genus *Xinidium* Harold, 1869a

Type species and designation: *Xinidium dentilabris* Harold, 1869a, by monotypy.
Synonyms: = *Parapinotis* Harold, 1878; Type species: *Parapinotis dewitzi* Harold, 1878, by monotypy.
Last review: Generic and species revision (Cambefort 1985a) with one species added subsequently (Cambefort 1993).

Xinidium Harold, 1869a was created for a single species to which three other species have been added subsequently; one described under the synonymous generic name, *Parapinotis* Harold, 1878. The genus is endemic to wet highlands of SE Africa where three species are endemic to South Africa and one to Zimbabwe. *Xinidium* species are macropterous and probably all show flight activity during darkness. All species tunnel from under droppings, but their nesting behaviour is unknown. Pasture species readily colonise cattle dung.

In South Africa, one species is assessed as Least Concern (LC) as it shows a wide occurrence in grasslands, mainly on wet E central highlands. The other two are associated with upland and highland forest patches. Although assessed as Data Deficient (DD), they may deserve an IUCN threat status approaching Vulnerable (VU).

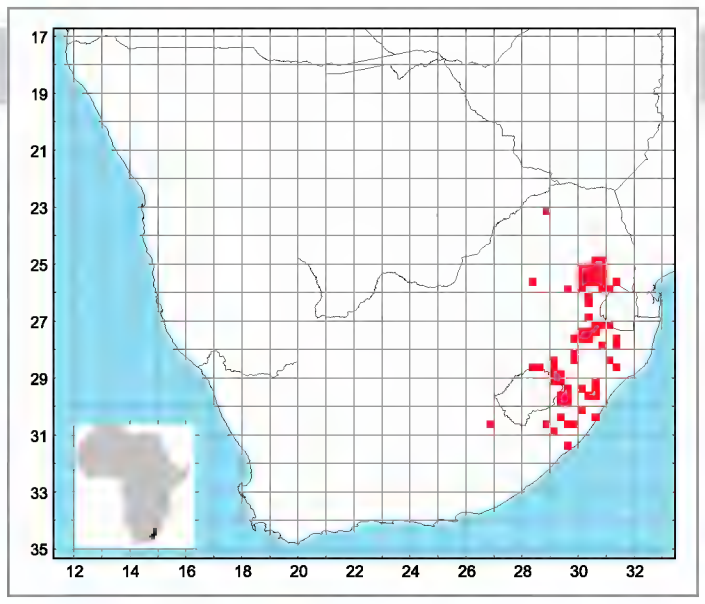
Xinidium dentilabris

Harold, 1869a

= *Copris curvifrons* Péringuey, 1885
= *Parapinotis dewitzi* Harold, 1878, *sensu* Péringuey, 1901 (*pars*)

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: 'Port. Natal.' [Durban, South Africa]; *C. curvifrons*: 'Limpopo River' [inexact locality; N South Africa / S Zimbabwe]; *P. dewitzi sensu* Péringuey, 1901: 'Natal (Durban, Estcourt), Southern Rhodesia (Victoria Falls)' [South Africa; Zimbabwe; latter citation is undoubtedly an error].

Taxonomy: Accepted species; sexual dimorphism (head, disc of prothorax); prominence of characters varies with body size; inexact type locality and original description suggest *C. curvifrons* is a synonym of *X. dentilabris* Harold, 1869 (known from the Soutpansberg close to Limpopo River), rather than *X. dewitzi*; Péringuey's 1901 description of *P. dewitzi* is also *X. dentilabris* (see Cambefort, 1985).

Distribution: Centred along the E escarpment of Mpumalanga, KwaZulu-Natal and NE Eastern Cape, South Africa in both cool, wet grasslands and forest; some coastal records in the S reflected by the type locality; Péringuey's, Zimbabwe type locality would represent misidentification (not *Xinidium*).

Locality data (mean ± SD, range): Altitude: 1 394 ± 452, 58–2 392 m; annual rainfall: 838 ± 110, 553–1 271 mm; annual temperature (max. + min. /2): 15.5 ± 2.1, 9.9–18.7°C (N=103).

Habitat: No adequate quantitative assessment; along an altitudinal grassland gradsect from 500 to 2 800 m in S KwaZulu-Natal; sampled primarily at 1 500 m and not at higher altitude (500 m: 0.2; 1 000 m: 2.2; 1 500 m: 19.1; 1 900 m: 0.2); at Carolina: sampled to cattle dung in greater numbers in improved Kikuyu pastures (4 163) and fallow crop fields (2 976) than in natural *Themeda* grassland (1 433); DBRU collection records from sand (1), sandy loam (7), sandy clay loam (18), clay (3) in grassland/pasture (23), forest (2); also fallow crop field (1).

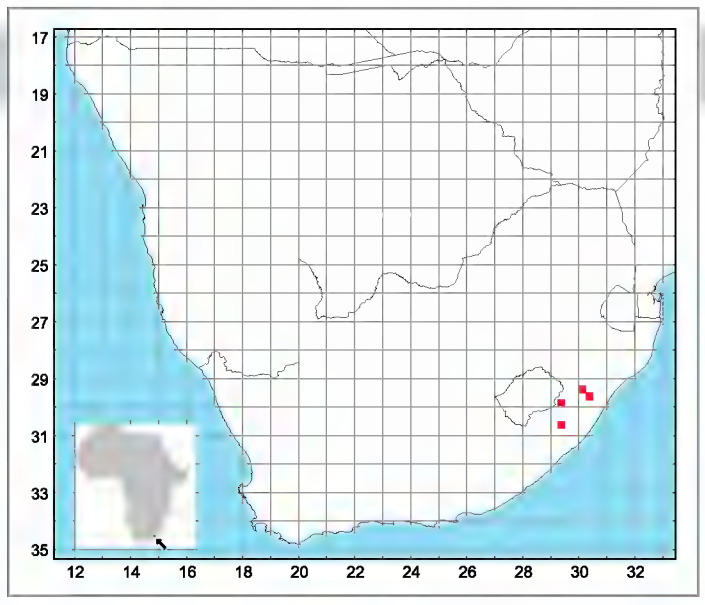
Food types: In upland forest at Mariepskop (1 505–1 554 m): clear bias to 14 pig dung samples (208) compared to cattle dung (38); DBRU collection records primarily from cattle dung (31), human/cattle dung mix (1).

Temporal activity: Flight activity during darkness, primarily during the summer rainy season (Oct. to May).

Bioregions South Africa: Primarily E Mesic Highveld Grassland (Gm), N Sub-Escarpment Grassland (Gs) (Grassland Biome); S Indian Ocean Coastal Belt Biome (CB); marginal in three other bioregions.

Assessment rationale: EOO = 107 815 km^2; available data suggest a bias to finer-grained soils with relatively generalist vegetation associations characterised by tolerance of pasture improvement and disturbance on farms where they are attracted to cattle dung in abundance despite a measured bias to omnivore dung; also occupy a sizeable range; therefore, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on vegetation associations measured at a standard altitude around 1 500 m; protected in Golden Gate National Park and Mount Sheba Nature Reserve.



Xinidium dewitzi

(Harold, 1878)

No synonyms (see taxonomic notes, *X. dentilabris*, Harold 1869a)

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Parapinotis dewitzi*: 'Cap der guten Hoffnung' [probably inaccurate; Cape of Good Hope, South Africa].

Taxonomy: Accepted species; strong sexual dimorphism (head, disc of prothorax); prominence of characters varies with body size.

Distribution: Presumably forest patches within grasslands on the E escarpment, KwaZulu-Natal, South Africa; citation from Zimbabwe is undoubtedly an error (see taxonomic notes under *X. dentilabris* Harold, 1869a).

Locality data (mean ± SD, range): Altitude: 1 287 ± 269, 999–1 645 m; annual rainfall: 813 ± 37, 765–847 mm; annual temperature (max. + min. /2): 15.1 ± 1.5, 13.1–16.7°C (N=4).

Habitat: No quantitative assessment; one DBRU collection record from sandy loam in pasture; one record from mistbelt forest.

Food types: No quantitative assessment; one DBRU collection record from cattle dung.

Temporal activity: Diel flight activity unknown, but probably in darkness during the summer rainy season (Jan. to Mar.).

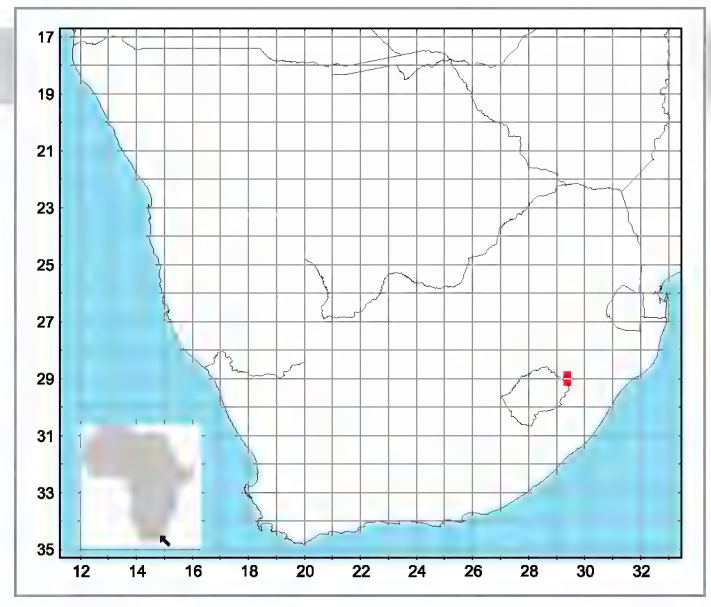
Bioregions South Africa: Three inexact localities map onto Drakensberg Foothill Moist Grassland (Gs 10) or Midlands Mistbelt Grassland (Gs 9) (Sub-Escarpment Grassland Bioregion, Grand Biome); one exact locality maps onto Southern Misbelt Forest (FOz 3).

Assessment rationale: EOO = 5 990 km^2; AOO probably much smaller, centred on upland forest patches although quantitative support is lacking; available observational data in conflict, therefore, assessed as Data Deficient (DD); however, an IUCN threat category of Vulnerable (VU) would be justified due to the low number of known localities within a small EOO coupled with a single exact locality suggesting primarily forest associations and a very small fragmented AOO.

Conservation measures: Assessment of conservation status requires quantitative data to determine the full EOO, AOO and ecological associations; one exact locality coincides with 40 ha of indigenous forest on iNhlosane Mt; unknown if any localities are officially conserved.

Xinidium howdeni

Cambefort, 1993



No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Afrique du Sud, Natal', '75 km WSW Estcourt, Cathedral Peaks Forest. Stn' / 'Rainbow Gorge...' [KwaZulu-Natal, South Africa].

Taxonomy: Accepted species; strong sexual dimorphism (head, disc of prothorax); prominence of characters varies with body size.

Distribution: Drakensberg highlands, NE border of Lesotho and KwaZulu-Natal, South Africa.

Locality data (mean ± SD, range): Altitude: 1 707 ± 186, 1 500–1 860 m; annual rainfall: 768 ± 59, 726–810 mm; annual temperature (max. + min. /2): 10.9 ± 2.5, 9.2–12.7°C (N=2).

Habitat: No quantitative assessment; no soil type data; type locality in podocarp forest at 1 500 m (altitude possibly underestimated) and in the *veld* [?grassland] at 1 860 m; data insufficient to determine if *X. howdeni* occurs only in forest patches known to also occur at high altitude around Botha's Shelter (Ndedema Gorge) (1 760 m) and the meteorological station on the Little Berg (1 860 m) (paratype localities).

Food types: No quantitative assessment; recorded on hyrax dung.

Temporal activity: Diel flight activity unknown, but probably in darkness during the summer rainy season (Dec.) like other *Xinidium* species.

Bioregions South Africa: One out of three grid references coincides with Northern Afrotemperate Forest (FOz 2) (Forest Biome); holotype locality recorded as forest but grid reference coincides with montane Drakensberg Grassland (Gd) (Grassland Biome).

Assessment rationale: EOO = ± 20 km^2 (presumably grossly underestimated); known from only the five individuals of the type series recorded at three localities; occurs at higher mean altitude than close grassland (*X. dentilabris* Harold, 1869) and forest relatives (*X. dewitzi* Harold, 1878) in KwaZulu-Natal; possibly a high altitude forest endemic; if so, AOO would be much smaller than EOO and it could qualify for an IUCN threat category despite some measure of protection; currently very poorly known and assessed as Data Deficient (DD).

Conservation measures: A quantitative survey of habitats on the slopes of the Drakensberg along the SE and NE Lesotho borders is required to determine the EOO, AOO and ecological associations before an assessment may be made of conservation status; many FOz 2 forest patches occur in this region and to the NW as far as S Mpumalanga; two of three known type localities lie within the Cathedral Peaks State Forest boundaries.

♂

Photographs: MNHN/A. Mantilleri.

♀

TRIBE GYMNOPLEURINI

Lacordaire, 1856

As Gymnopleurides; Type genus: *Gymnopleurus* Illiger, 1803.

The tribe, Gymnopleurini, is probably monophyletic. It occurs in the Afrotropical, S to E Palaearctic and Oriental regions. Species are found in Mediterranean to warm temperate to tropical climates where they occupy a range of habitats from arid to moist grasslands and savanna with a few in forest. All tribal members show diurnal, ball-rolling activity.

The Gymnopleurini are currently considered to comprise just four valid genera, of which three occur within and beyond the Afrotropical region: *Gymnopleurus* Illiger, 1903; *Allogymnopleurus* Janssens, 1940a; *Garreta* Janssens, 1940a. *Paragymnopleurus* Shipp, 1897b, is the fourth and most derived genus (Monaghan et al. 2007) with an Oriental and E Palaearctic centre of distribution.

Of three genera and 20 species found in South Africa, Botswana and Namibia, none is considered to be threatened.

(1) *Gymnopleurus* Illiger, 1803: Widely distributed genus in Afro-Eurasia represented in southern Africa by 12 species centred in SW Arid (3), upland grassland (2), Kalahari (1) or savanna (6) regions.

(2) *Allogymnopleurus* Janssens, 1940a: Widely distributed genus in the Afrotropical and Oriental regions represented by just two savanna species in southern Africa.

(3) *Garreta* Janssens, 1940a: Widely distributed genus in the Afrotropical and Oriental regions. It was represented in southern Africa by six species centred on savanna (3) savanna/upland grassland (1), or E forest (2) when this book was completed in 2017. Subsequently, two new southern African species were described (Davis & Deschodt 2018).

Genus *Allogymnopleurus* Janssens, 1940a

Type species and designation: *Gymnopleurus chloris* Klug, 1855, by original designation.
Synonyms: None.
Last review: Entire genus reviewed as an illustrated catalogue by Pokorný and Zídek (2009) with three synonymies.

The genus, *Allogymnopleurus* Janssens, 1940a, was created by subdivision of *Gymnopleurus* Illiger, 1803. It is currently represented by 18 valid species showing primarily savanna and upland grassland distributions in the Afrotropical (16) and Oriental regions (2).

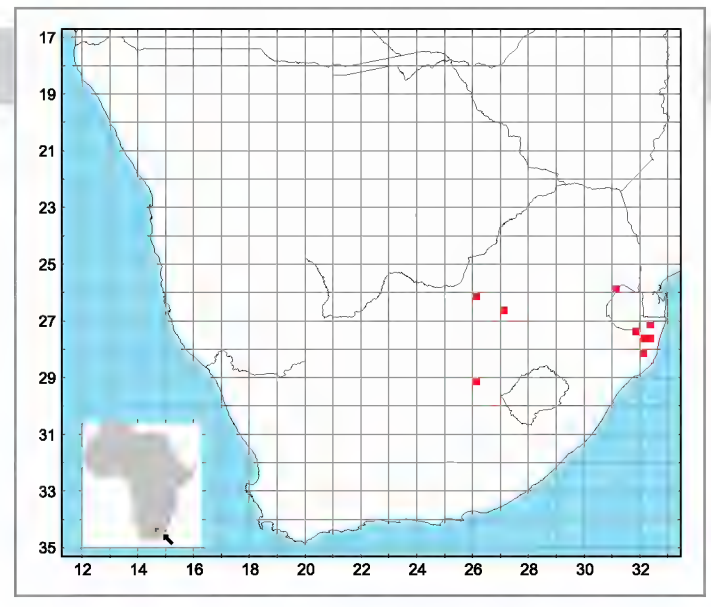
Relationships have not been investigated by phylogenetic analysis, although three groups may be recognised on the basis of fore tibial structure in males. One group bears an acute spine at the tip of the inner margin (see *A. splendidus* (Bertolini, 1849)), one bears a blunt or angular terminal swelling at the tip of the inner margin (see *A. consocius* (Péringuey, 1901)), and the other bears a crenulate inner margin. This may or may not have phylogenetic significance and may require re-interpretation.

Allogymnopleurus species are of moderate body size. They roll balls of dung away from droppings, often in pairs with the female pulling and male pushing. As the female constructs a single brood spheroid with a slight protuberance above the egg chamber on each breeding occasion, this strategy may be supported by small amounts of dung.

After the recent synonymy of *A. thalassinus* (Klug, 1855) and *A. chloris* (Klug, 1855) with *A. splendidus* (Bertolini, 1849), only two species are known to occur in Botswana, Namibia and/or South Africa. Both are centred on southern African savanna. One shows a large range in the E and smaller range in the W and is assessed as Least Concern (LC). The other is centred in the E with a range extending onto the Highveld and may have undergone range contraction.

Allogymnopleurus consocius

(Péringuey, 1901)

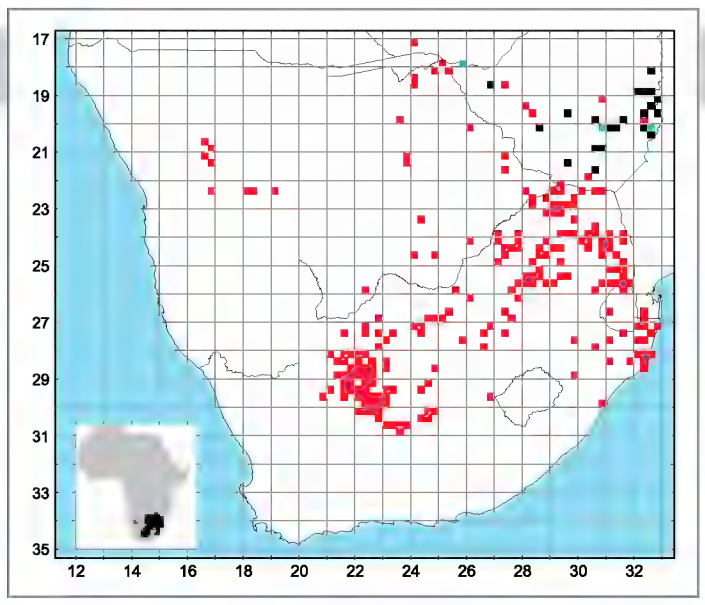


No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'Transvaal (Potchefstroom), Orange Free State (Bloemfontein)' [South Africa: North-West Province, Free State].
Taxonomy: Accepted species.
Distribution: Drier areas of NW South African Highveld and NE KwaZulu-Natal lowlands; regional colour variation with coastal individuals iridescent cupreous and Highveld individuals purple to violet.
Locality data (mean ± SD, range): Highveld: Altitude: 1 440 ± 73, 1 356–1 485 m; annual rainfall: 585 ± 44, 535–619 mm; annual temperature (max. + min. /2): 16.7 ± 0.9, 15.7–17.3°C (N=3). KwaZulu-Natal/Mpumalanga: Altitude: 202 ± 226, 55–722 m; annual rainfall: 757 ± 76, 661–900 mm; annual temperature (max. + min. /2): 21.5 ± 0.7, 20.3–22.4°C (N=8).
Habitat: In uMkhuze Game Reserve: extreme bias to clay (143.8) rather than sandy clay loam (1.4), duplex soils (sand over clay – 0.4) or sand (0.2); limited support from DBRU collection records: sandy loam (2), sandy clay loam (1), clay (1) in woodland (4).
Food types: No quantitative assessment; DBRU collection records from dung of wildebeest (1) and cattle (1).
Temporal activity: Diurnal flight activity in the summer rainy season (Oct. to Mar.).
Bioregions South Africa: Disjunct on Dry Highveld Grassland (Gh) (Grassland Biome) and S Lowveld (SVl) (Savanna Biome).
Assessment rationale: EOO = 35 250 km^2 (full range); AOO = 3 600 km^2 (current known range); described from the Highveld in 1901, but since 1970, only recorded on clay in open woodland in game reserves of coastal KwaZulu-Natal, particularly uMkhuze Game Reserve, where it is often found crowded together on wildebeest droppings, hence the species name *consocius*; qualifies for an IUCN threat category because of possible 90% range contraction to < 5 000 km^2, but until that is confirmed, assessed as Data Deficient (DD).
Conservation measures: Investigations are required to determine if apparent extreme contraction in range is a collection artefact or a true phenomenon justifying an IUCN threat category; a quantitative survey is required to confirm or negate its disappearance from former known localities on the South African Highveld, particularly vegetation types found in areas of clay soils; owing to observed association with blue wildebeest dung, research needs to be conducted on the possible role of wildebeest range contraction; protected in uMkhuze Game Reserve.



Allogymnopleurus splendidus

(Bertolini, 1849)

= *Gymnopleurus chloris* Klug, 1855
= *Gymnopleurus thalassinus* Klug, 1855
= *Gymnopleurus coracinus* Fahraeus, 1857
= *Gymnopleurus subcupratus* Fahraeus, 1857

Global: LC (see IUCN Red List – LC)*

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Gymnopleurus splendidus*: 'província Inhambanensi' [Inhambane Province, S Mozambique]; *G. chloris*: 'Sena' [Central Mozambique]; *G. thalassinus*: 'Tette' [Tete, Central Mozambique]; *G. coracinus*: 'in terra Natalensi' [KwaZulu-Natal, South Africa]; *G. subcupratus*: 'juxta fluvium Limpopo' [near Limpopo River, southern Africa].

Taxonomy: On the basis of precedence, the formerly accepted species (*A. thalassinus*, *A. chloris*) were synonymised with *A. splendidus* by Pokorný and Zídek (2009), having been recognised as comprising a single taxon showing considerable, mostly iridescent, colour variation; synonym *A. thalassinus* (red squares): black (N Namibia), cupreous and green varieties; synonym *A. chloris* (black squares): comprising shiny green varieties; varieties overlapping at NE edge of range (blue squares).

Distribution: Sandy savanna in arid upland to moist upland and lowland areas of southern Africa: N South Africa, N Central Namibia, E Botswana, Mozambique, Zimbabwe, Zambia; citations from Democratic Republic of the Congo (DRC), Tanzania require validation; Ethiopia, Kenya citations would represent confusion with *A. zavatarii* Müller, 1947.

Locality data (mean ± SD, range): Altitude: 956 ± 382, 0–1 958 m; annual rainfall: 477 ± 248, 133–1 659 mm; annual temperature (max. + min. /2): 19.5 ± 2.0, 13.4–25.9°C (N=413).

Habitat: On Gauteng bushveld: very strong bias to coarse-grained soils (deep sand: 198; sandy clay loam: 1) in open vegetation (grassland: 172; open woodland: 27; shaded thickets: 0); limited support from DBRU collection records on sand (38), sandy loam (28), sandy clay loam (11) in grassland/pasture (20), scrub/shrubland (26), open woodland (28).

Food types: At Phalaborwa: strong bias to omnivore compared to herbivore dung (pig: 1 046, elephant: 178, cattle: 358); DBRU collection records on dung of cattle (71), wildebeest (4), elephant (5), rhinoceros (3), zebra (1), warthog (1), horse (6), donkey (3), impala (1), human/cattle mix (1).

Temporal activity: Diurnal flight activity, primarily in the summer rainy season (Oct. to May); on Gauteng bushveld: peak activity early to mid-summer (Oct. to Jan.), tailing off in late summer (Feb. to Mar.); at Phalaborwa: greater abundance on a hot, dry day (944) than on a warm sunny day following heavy rainfall (380) or a warm cloudy day following light rainfall (129).

Ecoregions Namibia, Botswana, Zimbabwe, Mozambique: NW Kalahari Xeric Savanna (AT1309), Southern African Bushveld (AT0717), Zambezian and Mopane Woodlands (AT0725), Southern Miombo Woodlands (AT0719), Maputaland Coastal Forest Mosaic (AT0119), margins of other ecoregions.

Bioregions South Africa: Eastern Kalahari Bushveld (SVkb), Central Bushveld (SVcb), Mopane (SVl), Lowveld (SVl), N Sub-Escarpment Savanna (SVs) (Savanna Biome); NE Bushmanland (NKb), N Upper Karoo (NKu) (Nama Karoo Biome); N Dry Highveld Grassland (Gh) (Grassland Biome); N Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 1 523 410 km^2; SW range coincides with arid, little-transformed areas used primarily for grazing of domestic livestock (0–2% NK, W SVkb); NE range in regions with greater transformation (0–58% SV); at Phalaborwa: abundance greater in reserves (332) and farm rangeland (1 167) than in a mined area (83); assessed as Least Concern (LC). *IUCN Red List entry only for *A. chloris*.

Conservation measures: None required since *A. splendidus* is widespread and often abundant in farm rangeland; protected in various reserves including Kruger National Park and uMkhuze Game Reserve (South Africa).

Genus *Garreta* Janssens, 1940a

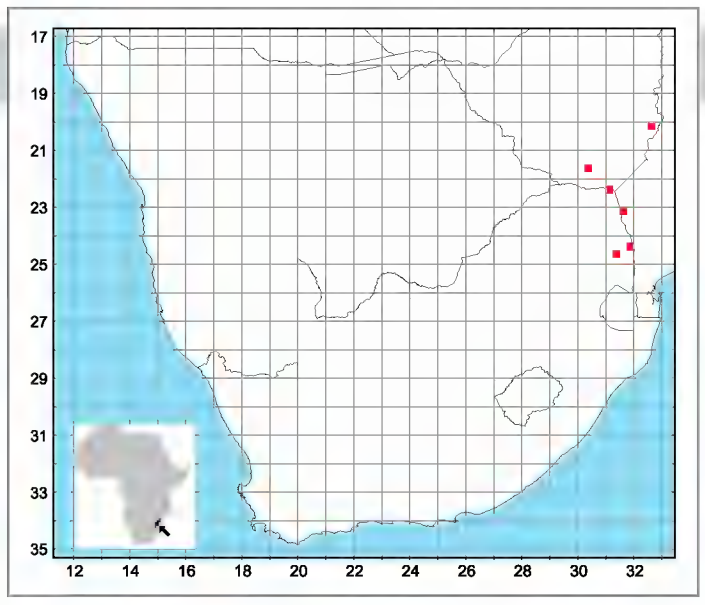
Type species and designation: *Ateuchus azureus* Fabricius, 1801, by original designation.
Synonyms: None.
Last review: Entire genus created and reviewed by Janssens (1940a); three new species subsequently added by Balthasar (1961b), Frey (1967, now synonymised) and Mittal (2011); two species complexes radically revised by Moretto and Génier (2015) with one synonymy in a third species group; revision of African species (Pokorný & Zídek 2018); two new species added by Davis and Deschodt (2018).

The genus, *Garreta* Janssens, 1940a, was created by subdivision of *Gymnopleurus* Illiger, 1803. When this book was completed at the end of 2017, the genus was represented by 23 valid species showing savanna or forest distributions in the Afrotropical (13) and Oriental regions (10). Subsequently, revision of the African component (Pokorný & Zídek 2018) and addition of species (Davis & Deschodt 2018) raises the African fauna to 15 species. There is no phylogeny nor have any groups been formally defined for the genus.

Garreta species are of moderate body size and are all macropterous showing diurnal flight activity. They roll balls of dung away from droppings, often in pairs with the female pushing and male pulling. As the female constructs a single brood spheroid with a slight protuberance above the egg chamber on each breeding occasion, this strategy may be supported by small amounts of dung.

Following the partial revision of Moretto and Génier (2015), six valid species are listed, here, for South Africa, Botswana and Namibia. Changes to the validity of some of these species following subsequent revision (Pokorný & Zídek 2018) or addition of new species (Davis & Deschodt 2018) are noted in the relevant species accounts. Although *G. fastiditus* (Harold,1867b) remains listed as valid by Pokorný & Zídek (2018), it is omitted from the species accounts for southern Africa as its type locality is considered an error. It may be a synonym of the Oriental *G. mundus* (Wiedemann, 1819).

Described southern African species are centred in moist savanna (4) or forest (2). The savanna species are centred in the west (1), east (2) or east extending onto the Highveld (1). Both forest species are centred in the east. Two species from savanna (1) or forest (1) show distributions extending into the tropics. All but one species show widespread occurrence and are assessed as Least Concern (LC – 5) or Data Deficient (DD – 1).



Garreta australugens

Davis & Deschodt, 2018

Global: DD

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: Wildlife College, Site 3, S24°32'27" E31°20'23" [South African Wildlife College, Kruger National Park, South Africa].

Taxonomy: Accepted species from southern Africa; recently separated from *Garreta lugens* (Fairmaire, 1891) described from East Africa 'la côte orientale d'Afrique vers le 1er degré de latitude nord…entre les pays Somalis et le pays de Massai' [probably NE lowlands of central Kenya].

Distribution: Moderately dry, hot, eastern lowlands in southern Africa: Mozambique, E Zimbabwe, NE South Africa.

Locality data (mean ± SD, range): Altitude: 405 ± 301, 96–1 020 m; annual rainfall: 659 ± 318, 383–1 177 mm; annual temperature (max. + min. /2): 22.6 ± 2.0, 19.0–24.8°C (N=7).

Habitat: No quantitative assessment; one DBRU collection record from sandy clay loam; near Orpen, Kruger National Park: three individuals sampled on sandy clay loam in very open woodland.

Food types: No quantitative assessment; one DBRU collection record from cattle dung.

Temporal activity: Diurnal flight activity in the summer rainy season (Nov., Dec.).

Ecoregions Zimbabwe: Zambezian and Mopane Woodlands (AT0725).

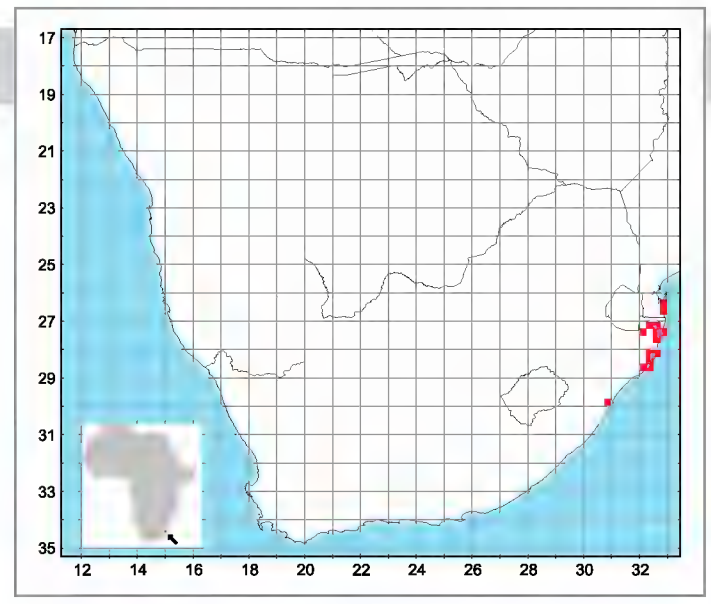
Bioregions South Africa: Centred on Mopane (SVmp) (Savanna Biome).

Assessment rationale: EOO = 88 890 km^2; widespread with population density apparently low even in the reserves where most of the reference material has been sporadically recorded; therefore, poorly known and assessed as Data Deficient (DD).

Conservation measures: Before an assessment may be made of conservation status, a survey of E lowlands is required to generate quantitative ecological data; currently protected in several national parks: Kruger (South Africa), Gorongosa (Mozambique).

Garreta caffer

(Fahraeus, 1857)



No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Gymnopleurus caffer*: 'in terra Natalensi' [KwaZulu-Natal, South Africa].

Taxonomy: Accepted species but exoskeleton sculpture differs only very slightly from that of the tropical south central African *G. laetus* subsp. *olivaceus* (Quedenfeldt, 1884) and Lake Malawi *G. nyassicus* (Kolbe, 1897); see notes on viewpoint of Pokorný & Zídek (2018) in section 9 of Preamble; support from a molecular phylogeny would be useful; *G. caffer* shows iridescent colour variation: mostly green, but also cupreous.

Distribution: Vegetation offering shade on the coastal deep sands of SE Africa: NE KwaZulu-Natal, South Africa; SE Mozambique (but see Taxonomy).

Locality data (mean ± SD, range): Altitude: 12 ± 23, 0–88 m; annual rainfall: 849 ± 114, 659–1 010 mm; annual temperature (max. + min. /2): 22.0 ± 0.5, 20.5–22.5°C (N=26).

Habitat: On deep sand at Richards Bay: recorded exclusively under shaded vegetation following mining, either regenerating or natural: grass/shrubland (0), younger woodland (17), older woodland (13), natural dune forest (32); on deep sand in Maputo Special Reserve: sampled primarily in cool coastal-fringing dune forest (24.6/trap) rather than warmer inland sand forest (large patch: 0.5, medium: 1.0, small: 0.1) or grassland (0); limited DBRU collection records from sand (1) in forest (1), grassland (1).

Food types: No quantitative assessment; no DBRU collection records; sampled to: mixed pig/cattle dung bait.

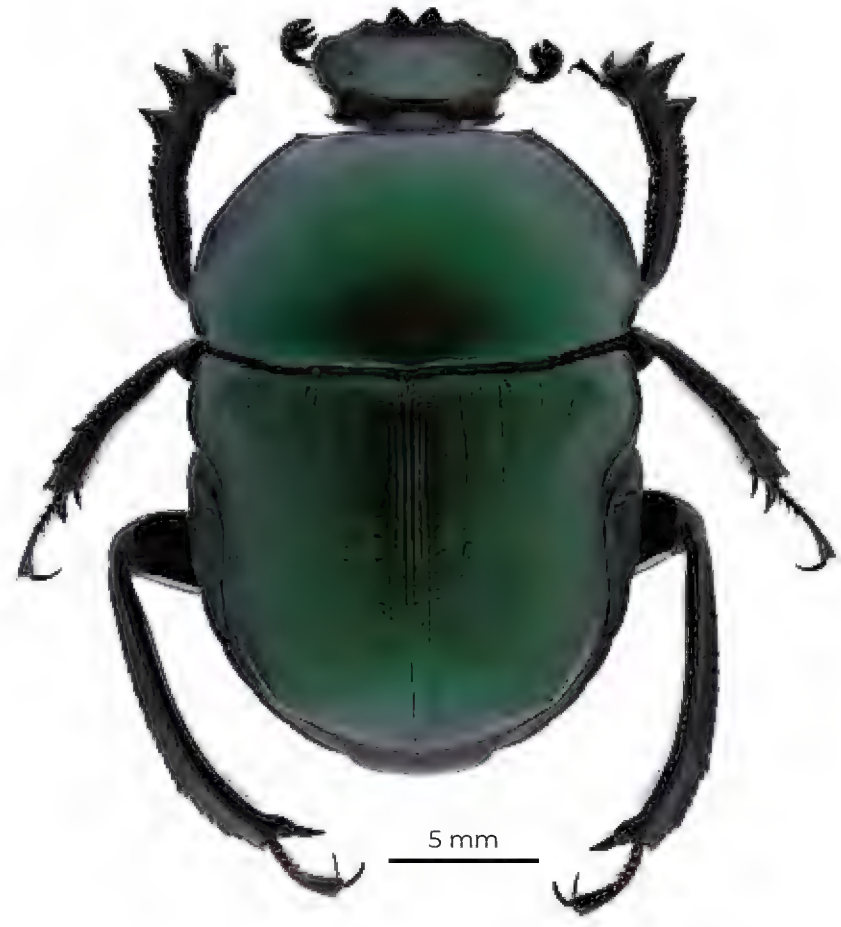
Temporal activity: Diurnal flight activity, primarily in the summer rainy season (Oct. to Feb.); also Aug. in warm coastal range.

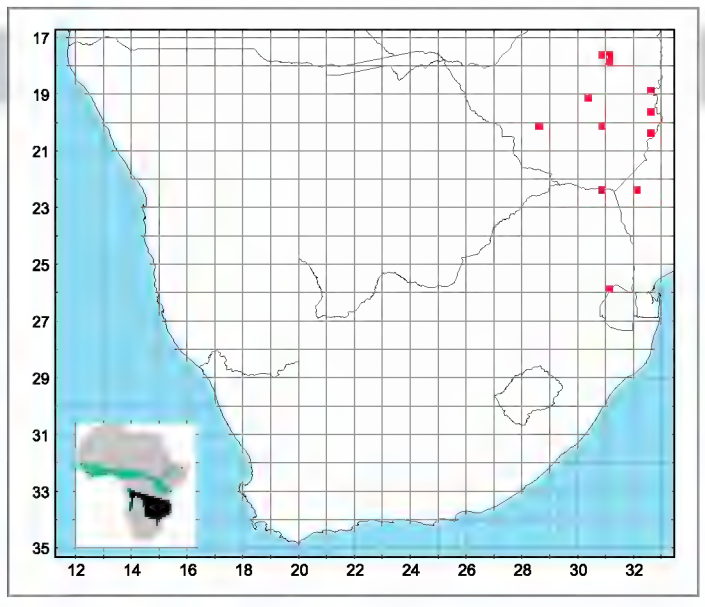
Ecoregions Mozambique: Centred on forest in Maputaland Coastal Forest Mosaic (AT0119).

Bioregions South Africa: N Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 8 394 km^2; AOO would be smaller due to habitat specialisation; largely centred on scattered patches of forest, particularly along the cooler coastline; all known records from deep sands; relatively small known range in a densely populated area, but assessed as Least Concern (LC) owing to extensive protection.

Conservation measures: Conservation status would be dependent on continuing protection of moist forest patches on the SE coast; assessment of status would be improved by quantitative data on AOO and associations with soil and dung type; protected in iSimangaliso Wetland Park (World Heritage Site) (South Africa), Maputo Special Reserve (Mozambique).





Garreta laetus

(Hope, 1842)

subsp. *laetus* (Hope, 1842)
= *Gymnopleurus cupreovirens* Kolbe, 1895
= *Gymnopleurus azureus* var. *cupreus* Kolbe, 1914
= *Gymnopleurus* (*Paragymnopleurus*) *azureus* var. *ebenus* Janssens, 1938
= *Gymnopleurus* (*Paragymnopleurus*) *azureus* var. *rubrocupreus* Janssens, 1938
subsp. *olivaceus* (Quedenfeldt, 1884)
= *Gymnopleurus insidiosus* Péringuey, 1901 (but see Taxonomy)

Global: LC (see IUCN Red List – LC as *G. azureus* (Fabricius, 1801))*

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: subsp. *laetus*: as *Gymnopleurus laetus*: 'vicinity of Cape Palmas' [Liberia]; *G. cupreovirens*: 'südöstliche vom Victoria-Njansa' [SE of Lake Victoria-Nyanza, Tanzania]; var. *viridimicans*: 'Undussuma, südwestlich vom Albert-Nyansa' [SW of Lake Albert, E central Africa]; var. *cupreus*: 'Am Westufer der Russisi, Nord-Tanganjika.... Kiwu-See (?)' [? Rusisi River, Lake Kivu, NW Tanzania]; var. *ebenus*: 'N.W.Tanganika' [NW Tanzania]; var. *rubrocupreus*: Not stated; subsp. *olivaceus*: as *Gymnopleurus olivaceus*: 'Malange' [N Angola]; *G. insidiosus*: 'Southern Rhodesia (Salisbury)' [Harare, Zimbabwe].

Taxonomy: Accepted species formerly listed under the name *G. azureus* (Fabricius, 1801) with exoskeleton sculpture that differs only very slightly from that of *G. caffer* (Fahraeus, 1857) on the SE African coast and *G. nyassicus* (Kolbe, 1897) from the environs of Lake Malawi; cited synonyms are those considered valid in a recent revision (Moretto & Génier 2015); however, the subspecies *olivaceus* is synonymised with *G. laetus* in the most recent review of Pokorný & Zídek (2018); molecular phylogenetic support would be useful; *G. laetus* shows iridescent colour variation: green, cupreous.

Distribution: subsp. *laetus* (range in green): W to E tropical Africa; subsp. *olivaceus* (range in black): tropical Africa S of the equatorial Congo rain forest reaching the extreme NE of South Africa: also Gabon, S Democratic Republic of the Congo (DRC), Angola, S Tanzania, N Mozambique, Zambia, Zimbabwe.

Locality data (mean ± SD, range): Altitude: 754 ± 594, 0–1 478 m; annual rainfall: 913 ± 275, 386–1 233 mm; annual temperature (max. + min. /2): 21.2 ± 3.1, 16.7–25.5°C (N=18).

Habitat: No quantitative assessment; DBRU collection records from sand (1) in forest (5).

Food types: No quantitative assessment; DBRU collection records from mixed human/cattle or buffalo dung bait (3), elephant dung (1).

Temporal activity: Diurnal flight activity, primarily in the summer rainy season (Sept. to May).

Ecoregions Zimbabwe, Mozambique: Centred on shaded vegetation in Southern Miombo Woodlands (AT0719), Southern Zanzibar-Inhambane Coastal Forest Mosaic (AT1028), Eastern Zimbabwean Forest Grassland Mosaic (AT1006); scattered records in shaded vegetation of Zambezian and Mopane Woodlands (AT0725).

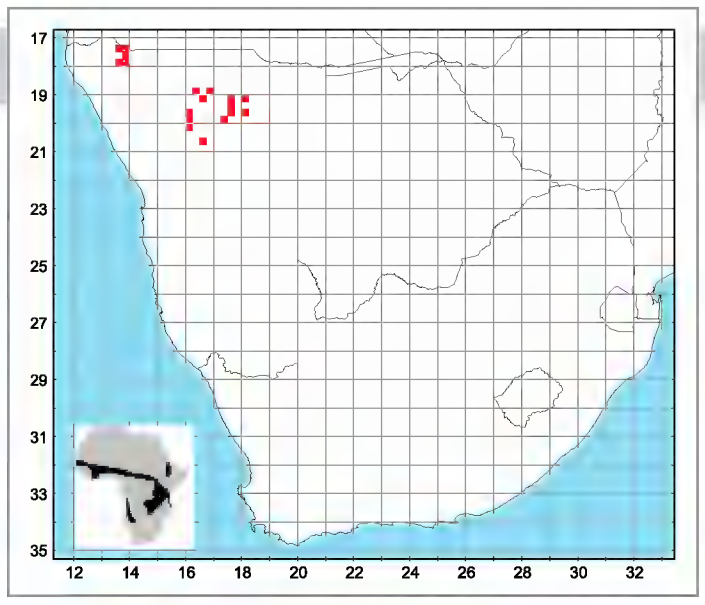
Bioregions South Africa: Marginal occurrence in shaded vegetation of Lowveld (SVl) (Savanna Biome).

Assessment rationale: subsp. *olivaceus* EOO = 2 848 875 km^2; widespread in southern tropical Africa, but as a forest specialist, AOO would be much smaller and subject to threat in some areas; however, owing to large range, currently assessed as Least Concern (LC); *IUCN Red List entry was assessed under the name *Garreta azureus* (Fabricius, 1801) before the revision of Moretto and Génier (2015) and incorporates both *G. laetus* and *G. caffer* (Fahraeus, 1857).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations and a survey of forest patches to determine the AOO; protected in Gorongosa National Park (Mozambique), Lake Mutirikwe Game Reserve (Zimbabwe), dense woodland in extreme NE of Kruger National Park (South Africa).

Garreta nitens

(Olivier, 1789)



= *Ateuchus azureus* Fabricius, 1801 (but see Taxonomy)
= *Gymnopleurus hilaris* Hope, 1842
= *Gymnopleurus janthinus* Castelnau, 1840
= *Gymnopleurus splendens* Castelnau var. *coeruleovirens* Kolbe, 1897
= *Gymnopleurus splendens* Castelnau var. *gracilipes* Kolbe,1897
= *Gymnopleurus splendens* Castelnau var. *kilimana* Kolbe, 1897

Global: LC (see IUCN Red List – LC)*

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Scarabaeus nitens*: 'Sénégal'; *A. azureus*: 'Guinea' [interpreted as Ghana]; *G. hilaris*: 'Sierra Leone'; *G. janthinus*: 'Barbarie, Tripoli' [Libya; probably inaccurate]; *G. splendens* var. *coeruleovirens*: 'Nyassa See' [Lake Malawi, Tanzania]; var. *gracilipes*: 'südöstliche vom Victoria-Nyansa' [SE of Lake Victoria-Nyanza, Tanzania]; var. *kilimana*: 'Kilimandscharo-Gebiet' [Mt Kilimanjaro region, Tanzania].

Taxonomy: Accepted species, but exoskeleton sculpture differs only very slightly from the SE African *G. wahlbergi* (Fahraeus, 1857), which has been considered a synonym until recently (Moretto & Génier 2015), and has now been synonymised once more with *G. nitens* (Pokorný & Zídek 2018); cited synonyms are those considered valid in the 2015 revision; however, *Ateuchus azureus* has since been revalidated (Pokorný & Zídek 2018) as *Garreta azureus* (Fabricius, 1801), a species apart from *G. nitens*; support from a molecular phylogeny would be useful; *G. nitens* shows iridescent colour variation from cupreous to green to blue.

Distribution: Varieties in three disjunct centres; (1) Dry to moist savanna of N Namibia, Angola: population may be isolated to SW of mega-Kalahari sands, disjunction within N Namibia probably real at moister localities on finer-grained soils separated by deep sands to N and NW of Etosha Pan; (2) Moist savanna of S Central to E to W Africa: 24 countries including Democratric Republic of the Congo (DRC), Zambia, Zimbabwe, Malawi, N Mozambique, Tanzania, Kenya, South Sudan, Nigeria, Benin, Togo, Ghana, Senegal; (3) NE Africa: Eritrea, Ethiopia.

Locality data (mean ± SD, range): Altitude: 1 282 ± 307, 683–2 196 m; annual rainfall: 545 ± 341, 356–2 097 mm; annual temperature (max. + min. /2): 20.4 ± 2.1, 13.8–23.2°C (N=26).

Habitat: No quantitative assessment; DBRU collection records biased to finer-grained soils: sand (1), sandy loam (2), sandy clay loam (2) in wooded habitat: shrubland (1), open woodland (4).

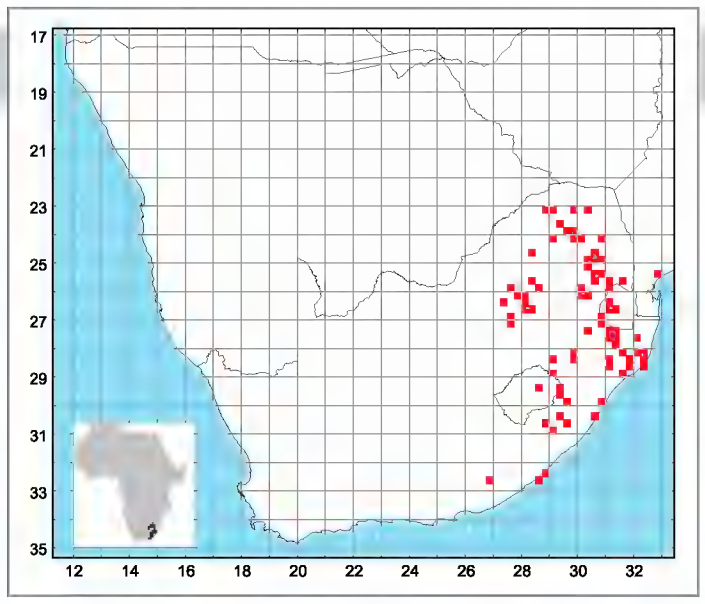
Food types: No quantitative assessment; DBRU collection records on herbivore dung: cattle (5), elephant (1), zebra (1).

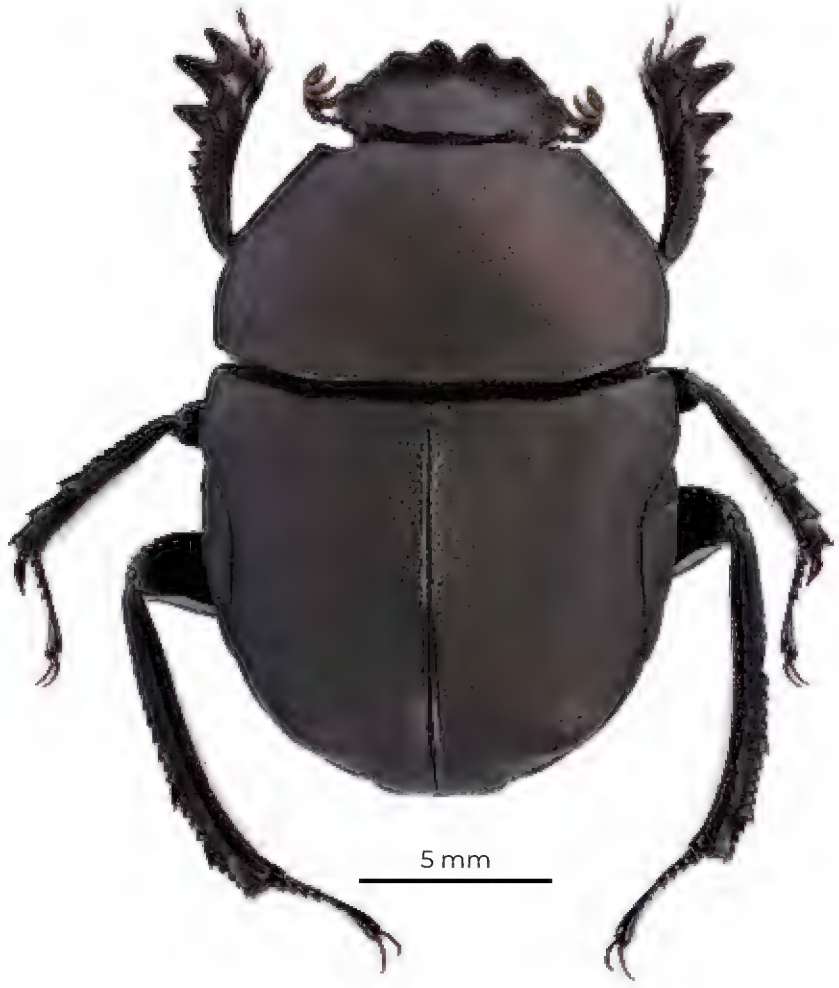
Temporal activity: Diurnal flight activity in the summer rainy season (Nov. to Apr.).

Ecoregions Namibia, Zimbabwe: Namibia: NE Namibian Savanna Woodlands (AT1316), S Angolan Mopane Woodlands (AT0702), margins of two other ecoregions; Zimbabwe: N Southern Miombo Woodlands (AT0719) (not shown on map).

Assessment rationale: EOO = 4 761 275 km²; further study would be useful to determine if exoskeleton structure varies along one or more clines within the range of *G. nitens* as well as across the transition to *G. wahlbergi*; AOO would be smaller than EOO due to bias to finer-grained soils and woody vegetation; loss of woodland would be a threat across its range; however, assessed as Least Concern (LC) because of very large EOO and coincidence with several reserves; *IUCN Red List entry for *G. nitens* includes data for *G. wahlbergi* (Fahraeus, 1857) as the assessment predates the recent 2015 revision.

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; protected in various national parks, including Etosha (Namibia).





Garreta unicolor

(Fahraeus, 1857)

= *Gymnopleurus delagorguei* Waterhouse, 1890

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Gymnopleurus unicolor*: 'Caffraria' [SE South Africa]; *G. delagorguei*: 'Port Natal' [Durban, South Africa].

Taxonomy: Accepted species, but taxonomy requires revision; often misidentified as *Garreta fastiditus* (Harold, 1867), which was described as originating from SE Africa, but type material is synonymous with an Oriental species, *G. mundus* (Wiedemann, 1819) (P. Moretto pers. comm.) (see generic notes).

Distribution: Centred on warmer, moist uplands and coastal hills bordering and encroaching onto the W, N and E South African Highveld (e.g. Magaliesberg, Waterberg, Blouberg, Soutpansberg, NE escarpment); marginal records suggest a distribution continuing N along moister parts of the SE Mozambique coastline; Zimbabwe citation would be *G. matabelensis* Janssens, 1938.

Locality data (mean ± SD, range): Altitude: 1 111 ± 626, 0–2 922 m; annual rainfall: 797 ± 114, 576–1 048 mm; annual temperature (max. + min. /2): 17.3 ± 2.8, 6.6–21.8°C (N=98).

Habitat: No quantitative soil assessment; on pig dung at Ithala Game Reserve, more abundant in highland grassland (191) than in mid-altitude grassland (114) or forest (4), lowland shrubland (74) or woodland (43); on Wolkberg at 1 400 m: extreme bias to grassland (139), forest (0); DBRU collection records biased to moderately fine-grained soils: clay (2), sandy clay loam (8), sandy loam (12), sand (5) in grassland/pasture (20), shrubland (3), open woodland (5), forest (1).

Food types: At Ithala Game Reserve: strong attraction to both omnivore and ruminant herbivore dung: pig (554), cattle (266), horse (61); DBRU collection records from various dung types: human/cattle mix (4), rhinoceros (2), horse (1), wildebeest (1), cattle (25).

Temporal activity: Diurnal flight activity in the summer rainy season (Oct. to Mar.).

Bioregions South Africa: In N: centred on moister vegetation units at the edge of the Grassland and Savanna Biomes, i.e. upland edges of Mesic Highveld Grassland (Gm), Central Bushveld (SVcb) and Lowveld (SVl) Bioregions, including mountains in the Central Bushveld; in SE: centred on Sub-Escarpment grassland (Gs) (Grassland Biome), Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 209 670 km^2; widespread and readily attracted to dung of domestic livestock although the range mostly coincides with vulnerable and endangered natural vegetation; transformation is extensive in some units of the highland grasslands where it is most abundant (Gm 33–67%, Gs 10–25%); however, recorded in various reserves so assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on soil associations and the impact of transformation through pasture improvement or creation of crop fields and tree plantations; protection offered in various game and nature reserves, including Hluhluwe–iMfolozi, Ithala, uMkhuze (sandy clay loam in open woodland on Lebombo Mts), Abe Bailey, Suikerbosrand and Vernon Crookes.

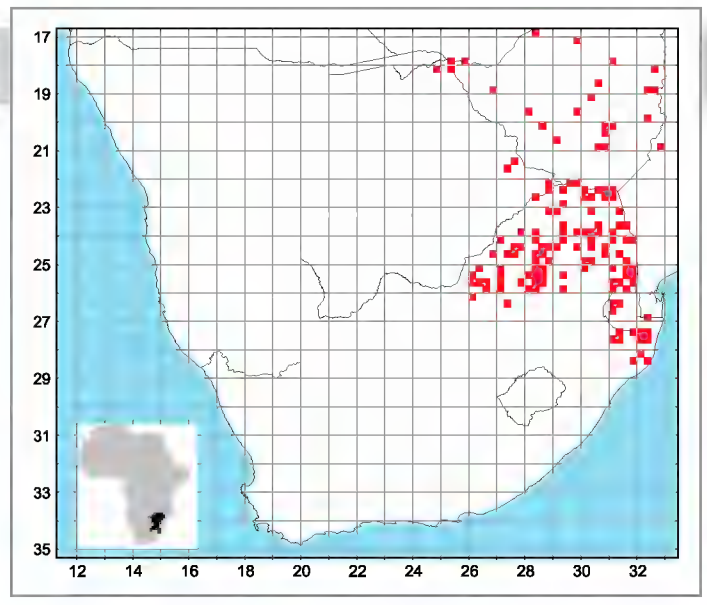
Garreta wahlbergi

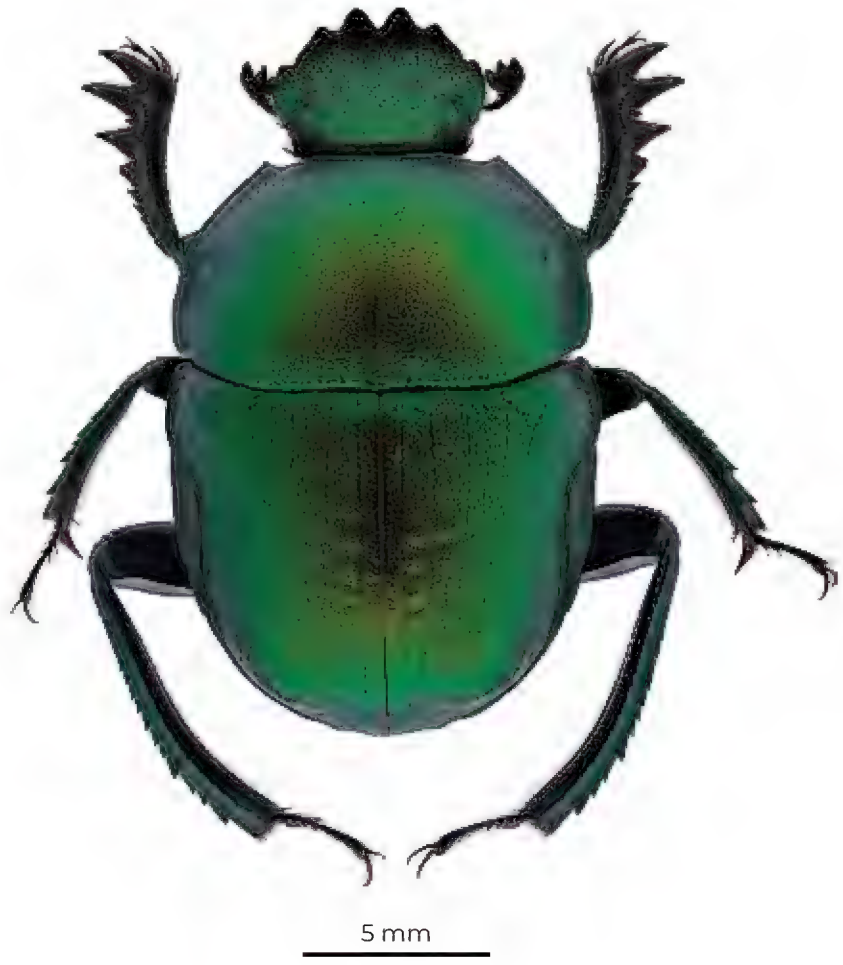
(Fahraeus, 1857) (but see Taxonomy)

= *Garreta zumpti* Frey, 1967

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J





Type localities: As *Gymnopleurus Wahlbergi*: 'in terra Natalensi', lectotype: 'Caffra / ria' [KwaZulu-Natal, South Africa]; *G. zumpti*: 'Transvaal, Rüstenburg und Umfolozi Zululand' [South Africa: Rustenburg, North-West Province; iMfolozi Game Reserve, KwaZulu-Natal].

Taxonomy: Accepted species (in 2017), but exoskeleton sculpture differs only very slightly from the tropical W, E and south central African *G. nitens* (Olivier, 1789) with which it has been synonymised until recently (Moretto & Génier 2015); now, synonymised once more by Pokorný and Zídek (2018), who regard the sculpture as intraspecific variation within *G. nitens*; support from a molecular phylogeny would be useful; *G. wahlbergi* shows iridescent colour variation from cupreous to green to blue.

Distribution: Widespread on finer-grained soils in woodland savanna of SE Africa: South Africa, Eswatini, NE Botswana, Zimbabwe, S Zambia, S Mozambique; Kalahari deep sands probably act as a barrier between ranges of *G. nitens* in N Namibia and *G. wahlbergi* to the E.

Locality data (mean ± SD, range): Altitude: 857 ± 441, 3–1 995 m; annual rainfall: 643 ± 142, 300–1 177 mm; annual temperature (max. + min. /2): 20.3 ± 2.3, 13.4–25.9°C (N=209).

Habitat: In Gauteng bushveld: strong bias to finer-grained soils: sandy clay loam (1 125), deep sand (12) in woody vegetation: shaded thickets (424), open woodland (634), grassland (75); similar bias in uMkhuze Game Reserve: sand (0.1), duplex soil (sand over clay) (2.4), sandy clay loam (7.6), clay (3.9); supported by DBRU collection records: clay (1), sandy clay loam (13), sandy loam (9), sand (1) in forest/thicket (11), open shrub/woodland (12), grassland/pasture (6).

Food types: At Phalaborwa: strong bias to dung of omnivores compared to herbivores: pig (332), cattle (50), elephant (25); DBRU collection records on various dung types: human/cattle mix (11), baboon (1), cattle (21), buffalo (2), wildebeest (1), elephant (10), rhinoceros (2), hippopotamus (1).

Temporal activity: Diurnal flight activity during the summer rainy season; in Gauteng bushveld: peak activity in early to mid-summer (Oct. to Jan.) tailing off into late summer (Feb. to Apr.); also recorded in autumn (May) at warmer coastline.

Ecoregions Botswana, Zimbabwe, Mozambique: Centred on Southern African Bushveld (AT0717), Zambezian and Mopane Woodlands (AT0725), S Southern Miombo Woodlands (AT0719); margins of adjoining ecoregions.

Bioregions South Africa: Centred on Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome); margins of four adjoining bioregions.

Assessment rationale: EOO = 737 635 km^2; readily attracted to cattle dung despite quantitative bias to omnivore dung; AOO biased by habitat specialisation to finer-grained soils and woody vegetation, which accounts for patchy distribution and absence from Kalahari deep sands; although clearance of woodland would be detrimental, assessed as Least Concern (LC) owing to widespread distribution across both farms and reserves; in South Africa, transformation, through cultivation varies from 0–58% (SVl), 2–49% (SVcb), 0–20% (SVmp).

Conservation measures: Conservation dependent on continuing conservation of woodland savanna on finer-grained soils; protected in Kruger National Park, uMkhuze and Hluhluwe–iMfolozi game reserves (South Africa), Hwange National Park (Zimbabwe).

Genus *Gymnopleurus* Illiger, 1803

Type species and designation: *Scarabaeus geoffroyi* Fuesslin, 1775, by subsequent designation (Reiche 1841).
Synonyms: = *Symnopleurus* Gebler, 1841, considered an error: misspelling of *Gymnopleurus*.
= *Spinigymnopleurus* Shipp, 1897b: Type species: *Gymnopleurus tristis* Castelnau, 1840, by original designation.
Last review: Entire genus reviewed by Janssens (1940a); new Afrotropical species added, subsequently: Ferreira (1954b), Balthasar (1963c), Endrödi (1976), Davis (1986); revision of one species group (Davis & Génier 2007).

Gymnopleurus Illiger, 1803 shows a distribution centred on the tropics and warm temperate regions of Afro-Eurasia. After removal of species into other genera in 1897 and 1940, it currently comprises 56 valid species found in the Afrotropical (35), Oriental (6), Palaearctic (12) regions, or shared between the Oriental and Palaearctic regions (3). These species include 10 now classified in the subgenus *Metagymnopleurus* Kabakov, 2006, which are centred on a single region or shared between regions as for the genus as a whole (4, 2, 1 or 3, respectively). There is no phylogeny to support relationships within the genus.

Gymnopleurus species are of moderate body size. They roll balls of dung away from droppings, often in pairs with the female pulling and male pushing. As a single pear-shaped brood is constructed in a chamber at the end of a shallow tunnel, they are able to breed using small amounts of dung. A number of species is found in arid regions where large droppings are often absent. Available data suggest a bias to omnivore dung in savanna species.

Gymnopleurus species are macropterous showing diurnal flight activity. A total of 12 valid species is known from South Africa, Botswana and Namibia although the validity of one species from central Namibia requires further investigation. Distributions of the remaining 11 species are mainly centred on hotter regions with none recorded from the winter and bimodal rainfall regions. Several are centred on the arid SW (3) or the Kalahari and pre-Namib sands (1). The remainder are mostly found in savanna, either centred in the east (4), widespread (1), widespread extending onto the Highveld (1), or restricted to the Highveld (1). Distributions of four savanna species extend northwards into the tropics, two characterised by disjuctions between N and S occurrences (although see taxonomic notes for *G. pumilus* Reiche, 1850).

Gymnopleurus species mostly occupy relatively large ranges. They are often abundant, particularly in drier, little-transformed regions. They have all been assessed as Least Concern (LC), except for one, particularly, poorly known species that is assessed as Data Deficient (DD).

Gymnopleurus aenescens

Wiedemann, 1821

= *Scarabaeus bufo* (Macleay, 1821)
= *Gymnopleurus cupreus* Fahraeus, 1857
= *Gymnopleurus aenescens* Wiedemann var. *capensis* Ferreira, 1954c

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *G. aenescens*: 'Prom. bon. sp.' [Cape of Good Hope, South Africa]; *S. bufo*: 'Cap Bonae Spei' [Cape of Good Hope]; *G. cupreus*: 'prope fluvium Limpopo' [close to Limpopo River, southern Africa]; var. *capensis*: 'Província do Cabo: Vryburg' [South Africa: Vryburg, North-West Province].

Taxonomy: Accepted species but individuals from the Kaokoveld (arid NW Namibia) should be compared with *G. vanderkelleni* van Lansberge, 1886 that was probably described from Angola and is currently synonymised in error with *G. virens* Erichson, 1843 (see, also, notes in Taxonomy section of *G. virens*).

Distribution: Sandy soils in open vegetation of southern African dry savannas: N South Africa, Namibia, Botswana, SW Angola, W Zimbabwe, S. Mozambique; outlier record from Gamkaberg (black square) requires validation.

Locality data (mean ± SD, range): Altitude: 978 ± 293, 9–1 782 m; annual rainfall: 354 ± 151, 22–738 mm; annual temperature (max. + min. /2): 19.8 ± 1.9, 13.3–23.4°C (N=157) (red squares only).

Habitat: On Gauteng bushveld: extreme association with coarse-grained soils: deep sand (19), sandy clay loam (0) and strong bias to open vegetation: grassland (14), open woodland (5), shaded thickets (0); partly supported by DBRU collection records: sand (12), sandy loam (5), sandy clay loam (1) in grassland (5) and scrub/shrub/woodland (10).

Food types: At Phalaborwa: strong bias to dung of omnivores compared to herbivores: pig (179), elephant (27), cattle (48); DBRU collection records on ruminant: cattle (10) and monogastric herbivore dung: elephant (1), rhinoceros (1), zebra (1), donkey (1).

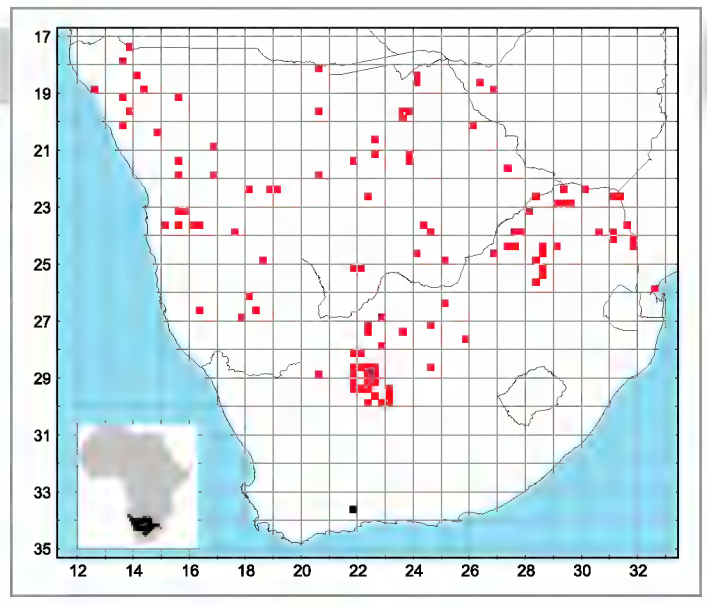
Temporal activity: Diurnal flight activity during the summer rainy season (Oct. to Mar.); at Phalaborwa: much greater activity in warm sunshine after heavy rainfall (195) than on a hot dry day (49) or cool cloudy day after light rainfall (8).

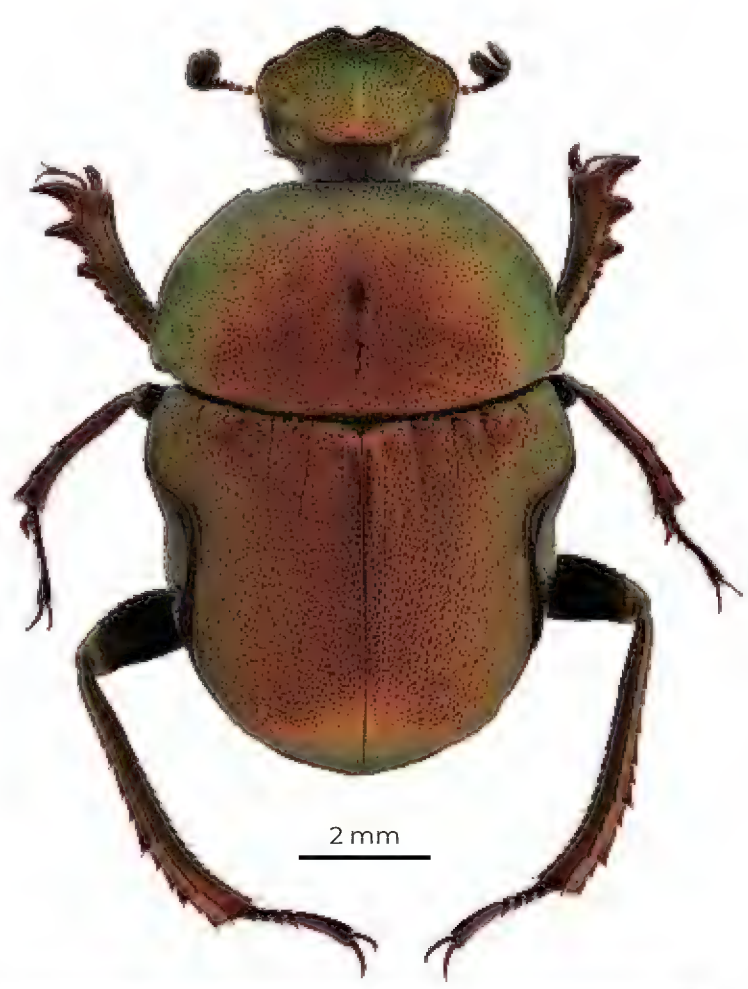
Ecoregions Namibia, Botswana, Zimbabwe, Mozambique: Namibian Savanna Woodlands (AT1316), Kalahari Xeric Savanna (AT1309), Angolan Mopane Woodlands (AT0702), Kalahari Acacia-Baikiaea Woodlands (AT0709), Southern African Bushveld (AT0717), Zambezian and Mopane Woodlands (AT0725), Maputaland Coastal Forest Mosaic (AT0119); marginal in four other ecoregions.

Bioregions South Africa: Centred on Mopane (SVmp), Central Bushveld (SVcb), Eastern Kalahari Bushveld (SVk) (Savanna Biome); marginal in NE Bushmanland (NKb), N Upper Karoo (NKu) (Nama Karoo Biome).

Assessment rationale: EOO = 1 407 890 km² (red squares only); widespread in drier sandy savanna, much of which is relatively untransformed and used for grazing of livestock to whose dung *G. aenescens* is frequently attracted despite a bias to omnivore dung; in South Africa: transformation limited in SW of range (0–2%, W SVk), greater in centre and NE (13–42%, E SVk; 3–48%, SVcb; 0–20%, SVmp).

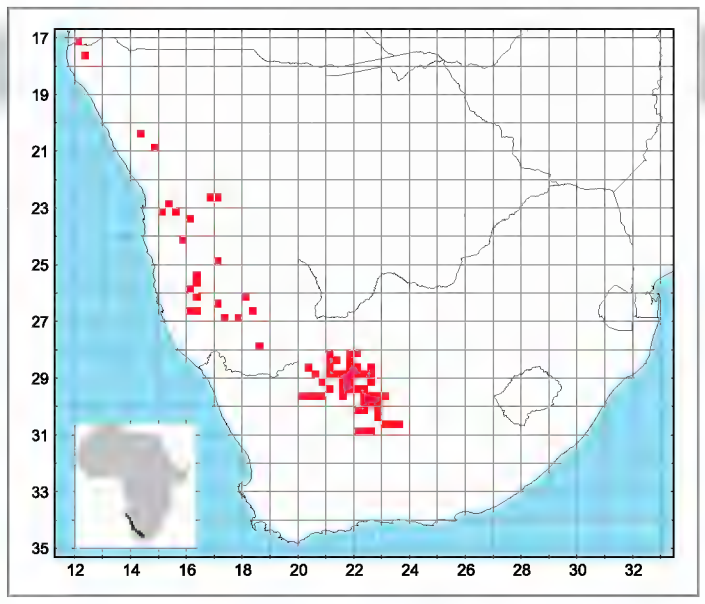
Conservation measures: None recommended; widespread in farm rangeland and game reserves; protected in Kruger National Park (South Africa), Chobe National Park (Botswana).





G. aenescens

G. vanderkelleni



Gymnopleurus andreaei

Ferreira, 1954b

No synonyms

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Prieska (Província do Cabo)' [South Africa: Prieska, Northern Cape].

Taxonomy: Accepted species; mostly uniformly deep purple; some greenish individuals at S edge of range.

Distribution: Arid late summer rainfall region in SW southern Africa; centred on climate types III1 and III2 of Walter and Lieth (1964); N central South Africa, W Namibia, SW Angola; less abundant at S edge of range than warmer N.

Locality data (mean ± SD, range): Altitude: 1 003 ± 220, 255–1 818 m; annual rainfall: 188 ± 54, 35–354 mm; annual temperature (max. + min. /2): 18.6 ± 1.4, 14.0–21.1°C (N=143).

Habitat: No quantitative assessment; in Northern Cape: centred on hot, arid Bushmanland (4.6/trap) rather than SW Kalahari deep sands (0.7) or cooler N Upper Karoo (0.5) although only shows a slight bias to finer-grained soils: sand (3.0/trap, n = 46 sites), sandy loam (6.7, n = 19); not supported by DBRU collection records: biased to sand (17), rather than sandy loam (2), in open vegetation: grassland/pasture (9), scrub/shrubland (8), open woodland (2).

Food types: No quantitative assessment; DBRU collection records: dung of baboon (1), donkey (3), horse (3), cattle (8), goat and sheep (1).

Temporal activity: Diurnal flight activity during the late summer rainy season (Feb. to Apr.).

Ecoregions Namibia: Centred on Namibian Savanna Woodlands (AT1316); marginal occurrence in two adjoining ecoregions.

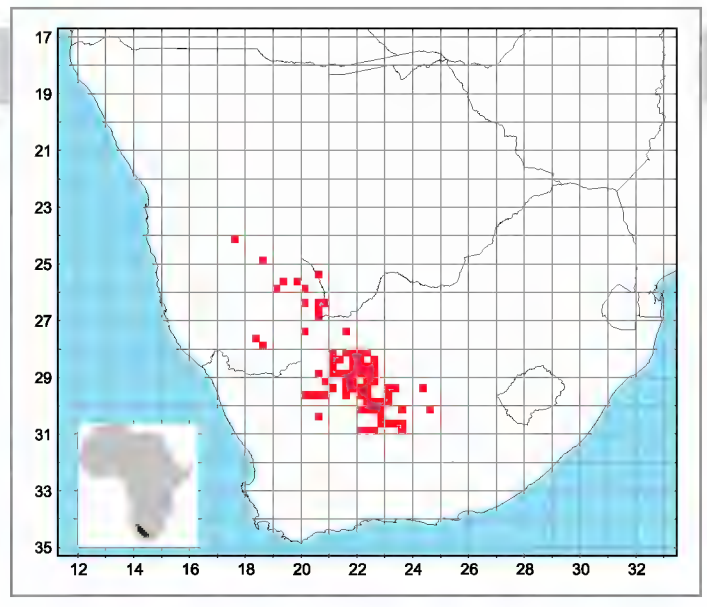
Bioregions South Africa: Centred on arid NE Bushmanland (NKb) (Nama Karoo Biome); marginal occurrence in two adjoining bioregions.

Assessment rationale: EOO = 263 705 km^2; widespread; entirely restricted to an arid area where transformation is limited and land usage is dominated by grazing of domestic livestock, primarily sheep; as collection records suggest fairly generalist soil and food associations, *G. andreaei* would face no threats; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on soil and dung type associations; protected in Iona National Park (Angola).

Gymnopleurus asperrimus

Felsche, 1909

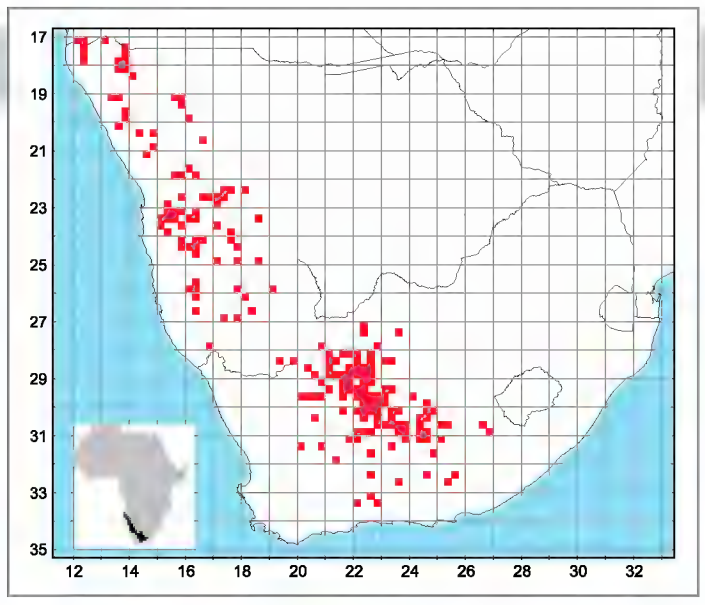


No synonyms

Global: LC
Endemic: RSA, Botswana, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Deutsch-Südwest-Afrika' [Namibia].
Taxonomy: Accepted species.
Distribution: Straddling borders of Namibia, Botswana and South Africa in southern part of the arid late summer rainfall region: climate types III1 and II(III)a of Walter and Lieth (1964).
Locality data (mean ± SD, range): Altitude: 1 020 ± 137, 684–1 508 m; annual rainfall: 206 ± 43, 114–353 mm; annual temperature (max. + min. /2): 18.9 ± 1.2, 14.7–21.3°C (N=187).
Habitat: No adequate quantitative assessment; in grassland, scrub and shrubland of the Northern Cape: primarily in SW Kalahari (6.8/trap), Bushmanland (13.4), and warm Karoo S of the River Orange (5.6) on sand (5.6/trap) and sandy loam / sandy clay loam (5.2); only partly supported by DBRU collection records on sand (21), sandy loam (2) in open woodland (1), scrub/shrubland (12), grassland/pasture (10).
Food types: No quantitative assessment; DBRU collection records on dung of cattle (12), donkey (3), horse (2).
Temporal activity: Diurnal flight activity during the late summer rainy season in the arid, late summer rainfall region (Jan. to Apr.).
Ecoregions Namibia: SW Kalahari Xeric Savanna (AT1309), Nama Karoo (AT1314).
Bioregions South Africa: Kalahari Duneveld (SVkd) (Savanna Biome); E Bushmanland (NKb), N Upper Karoo (NKu) (Nama Karoo Biome).
Assessment rationale: EOO = 223 500 km^2; shows an appreciable range in an arid area used primarily for the grazing of livestock where transformation is minimal (SVkd, NKb, NKu); also readily attracted to the dung of domestic livestock; assessed as Least Concern (LC).
Conservation measures: Assessment of conservation status would be improved by further quantitative data on ecological associations; protected in the South African part of Kgalagadi Transfrontier Park.



Gymnopleurus humanus

Macleay, 1821

= *Gymnopleurus sericatus* Erichson 1843
= *Gymnopleurus modestus* van Lansberge, 1886
= *Gymnopleurus modestus* Péringuey, 1888
= *Gymnopleurus peringueyi* Shipp, 1895b

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *G. humanus*: 'Cap. Bon. Spei.' [Cape of Good Hope, South Africa]; *G. sericatus*: 'Angola'; *G. modestus* van Lansberge: 'Benguela' [Angola]; *G. peringueyi nom nov.* for *G. modestus* Péringuey: 'Beaufort West, Cape Colony' [Western Cape, South Africa].

Taxonomy: Accepted polymorphic species; exoskeleton either blue, green or cupreous; as in other iridescent species, colour produced by selective reflection of different wavelengths of light by layers in the exoskeleton.

Distribution: Centred on the arid late summer rainfall region (climate types III1, III2, II(III)a, II(III)b, II4a) and arid parts of the bimodal rainfall region (III5) of Walter and Lieth (1964): SW central South Africa, Namibia, SW Angola; colour polymorphism correlates strongly with the cool, dry season, latitudinal temperature gradient: blue in cooler S; locally co-occurring blue, green or cupreous in N central Cape uplands; cupreous in warmer N; it has been suggested that differences in exoskeleton colour may be driven by the temperatures experienced during development (see Davis et al. 2008).

Locality data (mean ± SD, range): Altitude: 1 106 ± 282, 113–2 264 m; annual rainfall: 231 ± 86, 22–556 mm; annual temperature (max. + min. /2): 17.9 ± 1.9, 11.2–22.4°C (N=380).

Habitat: No adequate quantitative assessment; in Northern Cape: bias to hot arid Bushmanland (56.0/trap) compared to warm arid N Upper Karoo (24.5) or arid SW Kalahari deep sands (9.7); in Bushmanland: slight bias to finer-grained soils, sandy loam (68.4/trap), loamy sand (69.6), deep sand (37.6); opposite soil trend in DBRU collection records: sand (31), sandy loam (17), sandy clay loam (7) in grassland/pasture (13), scrub/shrubland (24), open woodland (12).

Food types: No quantitative assessment; DBRU collection records on dung of baboon (1), zebra (2), horse (5), donkey (2), cattle (36), sheep (2); sampled in abundance to pig dung.

Temporal activity: Diurnal flight activity in bright sunshine during the late summer rainy season (Dec. to May).

Ecoregions Namibia: Centred on Nama Karoo (AT1314), Namibian Savanna Woodlands (AT1316); also W margins of Kalahari Xeric Savanna (AT1309) and margins of four other ecoregions.

Bioregions South Africa: Bushmanland (NKb), Upper Karoo (NKu), Lower Karoo (NKl) (Nama Karoo Biome); W Eastern Kalahari Bushveld (SVkb) (Savanna Biome).

Assessment rationale: EOO = 587 750 km^2; widespread across a little-transformed arid region used primarily for the grazing of domestic livestock to whose dung *G. humanus* is readily attracted; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by additional quantitative ecological data, but in terms of abundance, a dominant species across much of its wide, little-transformed range; protected in several national parks, Namib-Naukluft and drier W of Etosha (Namibia), also Iona (Angola).

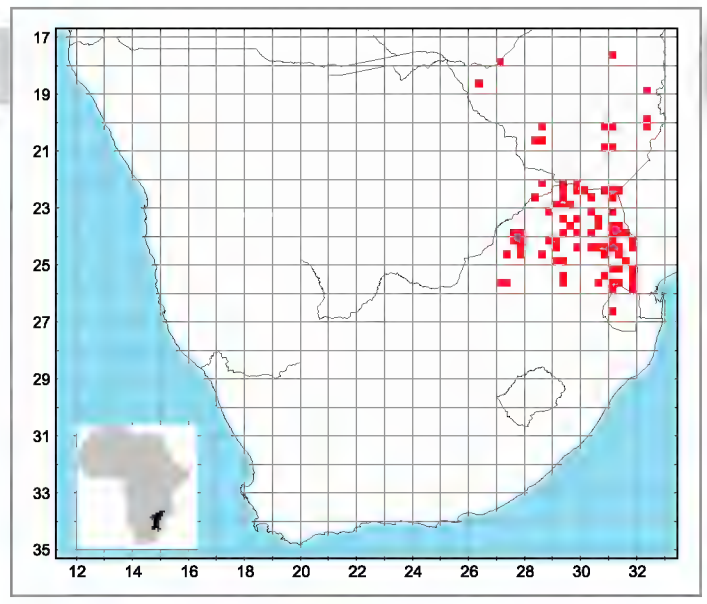
Gymnopleurus humeralis

Klug, 1855

= *Gymnopleurus humanus* Macleay, 1821, var. *azureus* Ferreira, 1954c

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: 'Tette' [Tete, Central Mozambique]; *G. humanus* var. *azureus*: 'Rodésia do Sul: Hillside' [possibly Hillside in Harare, Zimbabwe].

Taxonomy: Accepted polymorphic species; exoskeleton either iridescent blue, green or cupreous.

Distribution: Southern African wooded savanna: E Botswana, N South Africa, Eswatini, Zimbabwe, Mozambique, Malawi.

Locality data (mean ± SD, range): Altitude: 735 ± 368, 144–1 850 m; annual rainfall: 601 ± 158, 297–1 154 mm; annual temperature (max. + min. /2): 20.9 ± 2.0, 13.4–25.9°C (N=115).

Habitat: No quantitative assessment; DBRU collection records suggest a bias to fairly sandy soils: sand (8), sandy loam (12) in wooded savanna: grassland/pasture (2), open shrub/woodland (16); not found on the deep sands of the Kalahari; at Phalaborwa: more abundant in reserves (163) than farmland (5).

Food types: At Phalaborwa: strong bias to dung of omnivores compared to herbivores: pig (162), elephant (1), cattle (21); DBRU collection records on dung of omnivores: human (1), baboon (1); monogastric herbivores: elephant (5), rhinoceros (2), horse (1), donkey (1); and ruminant herbivores: cattle (9).

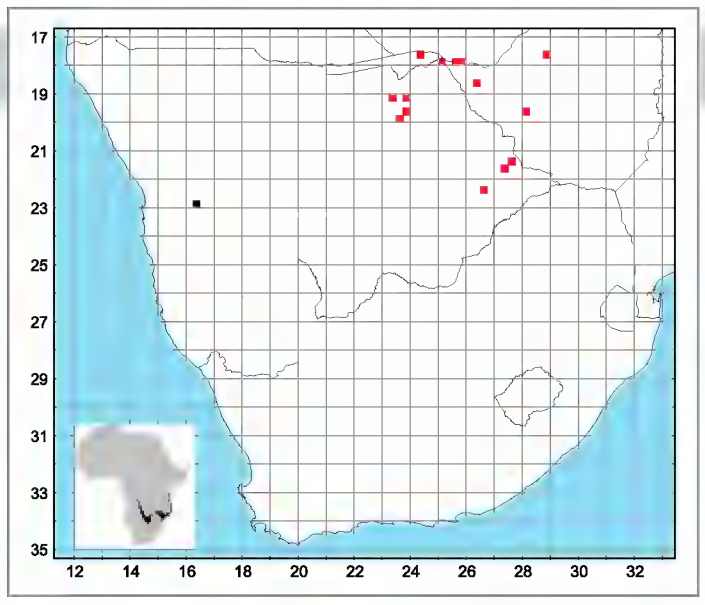
Temporal activity: Diurnal flight activity in the summer rainy season (Oct. to Apr.); at Phalaborwa: much more abundant on a hot, dry day (151) than on a warm sunny day after heavy rainfall (6) or a warm cloudy day after light rainfall (27).

Ecoregions Botswana, Zimbabwe: Zambezian and Mopane Woodlands (AT0725), Southern African Bushveld (AT0717), Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Central Bushveld (SVcb), Mopane (SVmp), N Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 534 260 km^2; although widespread, possible bias to woody savanna suggests clearance of woodland would have a negative influence on population density; unclear if the Phalaborwa results were influenced by vegetation density or dung type availability; currently widespread in reserves and farm rangeland, so assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on soil and vegetation associations; protected in various reserves including Kruger National Park (South Africa), Lake Mutirikwe Game Reserve (Zimbabwe).



Gymnopleurus ignitus

Klug, 1855

= *Gymnopleurus smaragdinus* Fahraeus, 1857
= *Gymnopleurus ignitus* Klug var. *laeviuscula* Kolbe, 1895
= *Gymnopleurus ignitus* Klug var. *nigrocupreus* Janssens, 1938a

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *G. ignitus*: 'Inhambane und Sena.....Tette' [Inhambane, Sena, Tete: Mozambique]; *G. smaragdinus*: 'prope fluvium Limpopo' [close to Limpopo River, southern Africa]; var. *laeviuscula*: 'Tanga, Pangani, Mombassa, Sansibar' [Tanga, Pangani, Zanzibar: Tanzania; Mombasa, Kenya]; *G. nigrocupreus*: 'Kikwit (Congo belge: Kwango)' [Bandundu Province, W Democratic Republic of the Congo (DRC)].

Taxonomy: Accepted polymorphic species; exoskeleton either iridescent green or cupreous; difficult to separate from more coarsely punctate examples of *G. pumilus* Reiche, 1850.

Distribution: Probably sandy soils in tropical savanna from S central to E Africa: W Democratic Republic of the Congo (DRC), N Namibia, N Botswana, Zimbabwe, Malawi, Mozambique, coastal Tanzania, coastal Kenya; Angola record requires validation, but is consistent with Democratic Republic of the Congo (DRC) record; may also occur in Limpopo Province, N South Africa; occurrence in central Namibia tentative (black square).

Locality data (mean ± SD, range): Altitude: 706 ± 400, 0–1 427 m; annual rainfall: 652 ± 225, 252–1 177 mm; annual temperature (max. + min. /2): 22.8 ± 1.9, 17.8–25.9°C (N=24).

Habitat: No quantitative assessment; limited DBRU collection records biased to sandy soils: deep sand (3), sandy loam (2) entirely in open woodland (5).

Food types: No quantitative assessment; limited DBRU collection records on various dung types: human (1), elephant (1), rhinoceros (1), warthog (1), donkey (1).

Temporal activity: Diurnal flight activity in the summer rainy season (Nov. to Apr.).

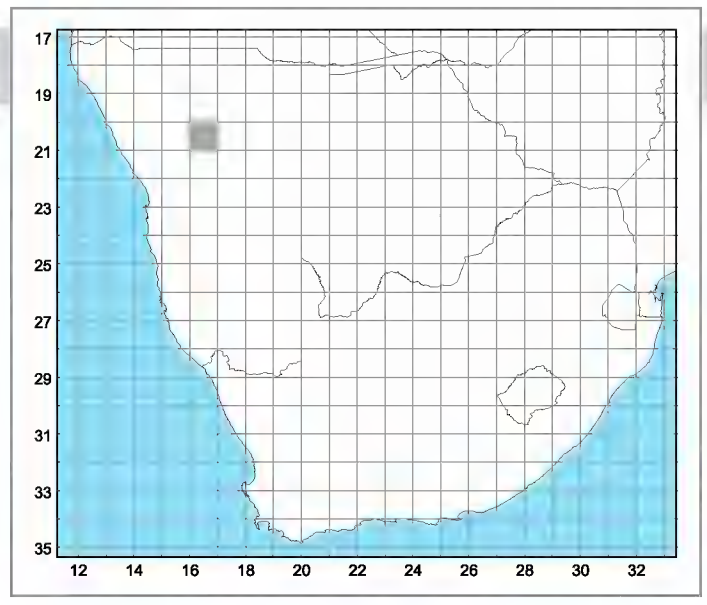
Ecoregions Namibia, Botswana, Zimbabwe: Zambezian Baikiaea Woodlands (AT0726), Zambezian and Mopane Woodlands (AT0725), Kalahari Acacia-Baikiaea Woodlands (AT0709), Southern African Bushveld (AT0717).

Assessment rationale: EOO = 659 605 km^2; as the AOO may be limited by occurrence of sandy soils and woodland, clearance of woodland might be detrimental to population density; however, quantitative support is required; occupies a large EOO; therefore, assessed as Least Concern (LC) although somewhat Data Deficient (DD).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, particularly support for specialist soil and vegetation associations, which would assist in determining the AOO; protected in several national parks: Chobe (N Botswana), Gorongosa (central Mozambique).

Gymnopleurus imitator

Balthasar, 1963c

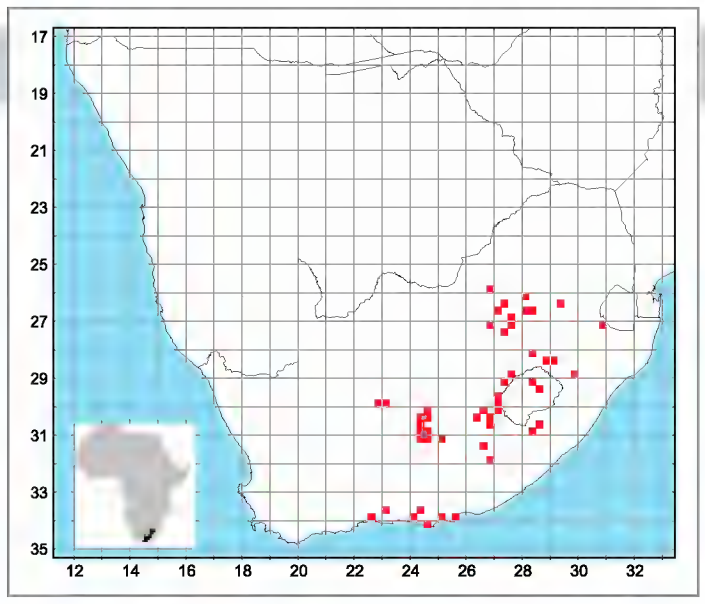


No synonyms

Global: DD
Endemic: Namibia

| J | A | S | O | N | D | J | F | M | A | M | J |

Type locality: 'Süd-Westafrika, Otjiwarongo-District' [Namibia].
Taxonomy: Accepted species, currently known only by the holotype; described as closely related to *G. sericatus* Erichson, 1843, and *G. humanus* Macleay, 1821, which are now considered synonyms (see *G. humanus* species account); further study required to determine taxon status but probably a synonym of the widespread *G. humanus*.
Distribution: Only known from Otjiwarongo District, Namibia (grey shaded area).
Locality data: No precise locality data.
Habitat: Not known.
Food types: Not known.
Temporal activity: Not known, presumably diurnal flight activity like other *Gymnopleurus* species; no seasonal data.
Ecoregions Namibia: Locality inexact, probably at S edge Angolan Mopane Woodlands (AT0702) / NE edge Kalahari Xeric Savanna (AT1309).
Assessment rationale: EOO unknown; a study is required to determine if this taxon is a valid species or a synonym of *G. humanus* with morphological characteristics representing only intraspecific variation; assessed as Data Deficient (DD).
Conservation measures: No assessment of conservation status is possible until taxonomic questions have been resolved; should its valid species status be upheld, quantitative data on EOO, AOO and ecological associations will be required to support an assessment.



Gymnopleurus leei

(Fabricius, 1792)

= *Gymnopleurus caelatus* Wiedemann & Germar, 1821
= *Gymnopleurus bicolor* Castelnau, 1840
= *Gymnopleurus macleayi* Castelnau, 1840
= *Gymnopleurus liechtensteini* Fahraeus, 1857

Global: LC
Endemic: RSA, Lesotho

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Scarabaeus leei*: 'Cap. Bon. Spei'; *G. caelatus*: 'Prom. Bon. Spei.'; *G. bicolor*: 'Cap de Bonne-Espérance'; *G. macleayi*: 'Cap' [all Cape of Good Hope, South Africa]; *G. liechtensteini*: 'Natal' [KwaZulu-Natal, South Africa].

Taxonomy: Accepted species.

Distribution: Centred on higher or cooler, often drier parts of the summer rainfall Highveld; also, NE Upper Nama Karoo; with apparent disjunct occurrence in the bimodal rainfall region along the S coast of the Eastern Cape, South Africa.

Locality data (mean ± SD, range): Altitude: 1 335 ± 408, 21–2 264 m; annual rainfall: 514 ± 174, 227–845 mm; annual temperature (max. + min. /2): 15.6 ± 1.5, 10.7–18.6°C (N=74).

Habitat: No quantitative assessment; DBRU collection records on sand (8), sandy loam (8), sandy clay loam (5) in grassland/pasture (10), scrub (1), open woodland (10) and old crop fields (3).

Food types: No quantitative assessment; DBRU collection records on dung: human/cattle mix (1), horse (1), cattle (30).

Temporal activity: Diurnal flight activity in the summer rainy season (Oct. to Mar.).

Bioregions South Africa: Centred on drier vegetation units in the cool Mesic Highveld Grassland (Gm); also moist Sub-Escarpment Grassland (Gs), Drakenberg Grassland (Gd) (Grassland Biome); moister NE parts of Upper Karoo (Nama Karoo Biome) and E vegetation units of Sandstone Fynbos (FFs) (Fynbos Biome).

Assessment rationale: EOO = 256 000 km^2; other than the NE Nama Karoo, the distribution coincides with vegetation units that are vulnerable or endangered; transformation 33–67% (Gm); records from old crop fields suggest some resilience to habitat transformation; however, at Viljoenskroon only sampled as a rarity in natural grassland (2), not in a crop field or improved pastures; assessed as Least Concern (LC) due to large range.

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; at least 80% of the range coincides with highly modified regions; therefore, quantitative data on effects of pasture improvement and other forms of transformation would be useful; only very small parts of the range are protected, e.g. Suikerbosrand and Abe Bailey nature reserves.

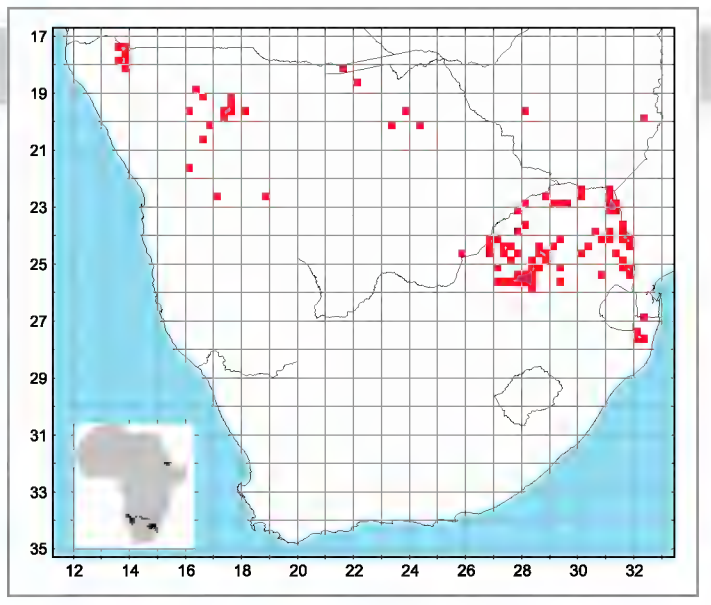
Gymnopleurus pumilus

Reiche, 1850 (but see Taxonomy)

= *Gymnopleurus gibbosus* Roth, 1851
= *Gymnopleurus virens* Erichson subsp. *sternalis* Müller, 1942

Global: LC (see IUCN Red List – LC)*

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: *G. pumilus*: 'Abyssinie' [Ethiopia]; *G. gibbosus*: 'abyssinien' [Ethiopia]; subsp. *sternalis*: 'Aethiopia meridionali' [southern Ethiopia].

Taxonomy: This species is often cited as *G. virens* Erichson, 1843, but does not match the type specimen; it more closely resembles species described from Ethiopia that are currently synonymised in error with *G. virens* (the oldest of these is *G. pumilus*); taxonomic revision is required to determine if southern African and Ethiopian populations represent two different species or a single widely distributed species with a disjunction across several thousands of kilometres; the exoskeletons of these populations are usually either iridescent yellow-green, green or cupreous in southern Africa and blue or violet in NE Africa; the prothoracic discs show an often ill-defined pattern of v- or u-shaped punctation and shiny apunctate patches; the punctation is usually moderately strong, but does vary in strength; it may be close to the very strongly patterned dense punctation of *G. ignitis* Klug, 1855, or to the weakly patterned fine punctation of the true *G. virens* (see species account).

Distribution: Disjunct distribution in hot dry savanna possibly partly related to soil and climatic specialisation rather than entirely to collection artefacts; NE Africa: Ethiopia; hiatus to southern Africa: N South Africa, Mozambique, Zimbabwe, N Botswana, N Namibia, SW Angola; record from Democratic Republic of the Congo (DRC) requires validation; record from Guinea presumably an error.

Locality data (mean ± SD, range): Altitude: 851 ± 435, 48–1 815 m; annual rainfall: 550 ± 113, 277–820 mm; annual temperature (max. + min. /2): 20.8 ± 1.7, 16.3–24.4°C (N=141).

Habitat: No adequate quantitative assessment; in uMkhuze Game Reserve: bias to finer-grained soils: sand (0.3), duplex soils (sand over clay) (1.4), sandy clay loam (1.4), clay (4.8); partly supported by DBRU collection records: sand (9), sandy loam (16), sandy clay loam (3), with a bias to open woodland (20) as opposed to shrubland (4) or grassland (4).

Food types: At Phalaborwa: strong bias to dung of omnivores: pig (190), rather than herbivores: elephant (26), cattle (47); DBRU collection records from a range of dung types: cattle (17), buffalo (1), wildebeest (1), waterbuck (1), impala (1), elephant (4), rhinoceros (2), donkey (1).

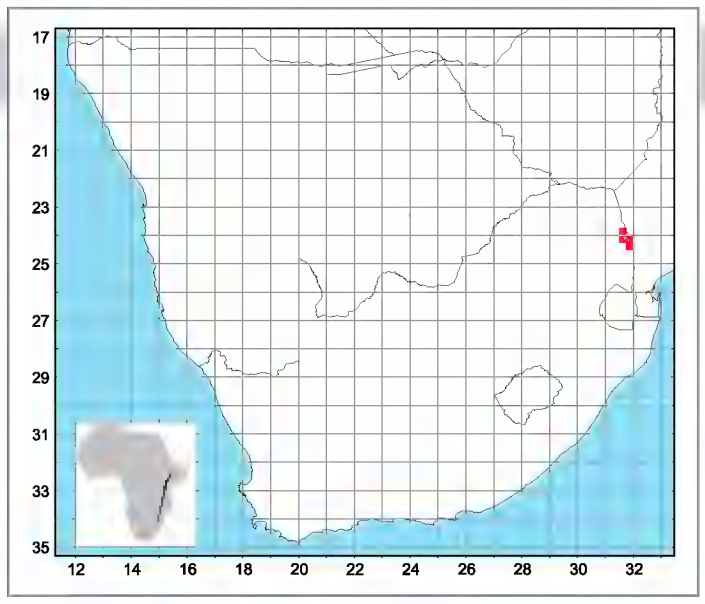
Temporal activity: Diurnal flight activity in the summer rainy season (Oct. to Mar.); at Phalaborwa: much greater abundance on a warm day soon after heavy rainfall (190) than on a warm cloudy day following light rainfall (26) or a hot dry day (47).

Ecoregions Namibia, Botswana, Zimbabwe: Angolan Mopane Woodlands (AT0702), NE Kalahari Xeric Woodlands (AT1309), NE edge Namibian Savanna Woodlands (AT1316), Zambezian and Mopane Woodlands (AT0725), Kalahari Acacia-Baikiaea Woodlands (AT0709).

Bioregions South Africa: Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 451 400 km² (underestimated gross estimate); AOO would be smaller due to soil and vegetation bias; data suggest two main southern African centres in N Namibia / SW Angola and N South Africa to NW and SE of the largely unfavourable deep Kalahari sands; dry woodland savanna range maybe influenced by clearance of trees; in South Africa, often extensive habitat transformation within its range (SVl: 0–58%, SVcb: 2–49%, SVmp: 0–20%); however, assessed as Least Concern (LC) owing to wide range and protection in reserves; *see IUCN Red List entry under *G. virens* Erichson, 1843, which includes data for this species.

Conservation measures: Taxonomic revision is required to correct errors in nomenclature; assessment of conservation status would also be improved by quantitative data on habitat associations; protected in Kruger National Park and uMkhuze Game Reserve (South Africa).



Gymnopleurus reichei

Waterhouse, 1890

No synonyms

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Abyssinia' [Ethiopia].

Taxonomy: Accepted species, but further investigation of the taxonomic status of the southern population would be useful.

Distribution: Dry highlands of NE Africa (N Kenya, Ethiopia) and dry lowlands of NE South Africa; South African population possibly an outlier rather than S limits of a continuous distribution; regional colour variation with known NE individuals violet and S populations cupreous.

Locality data (mean ± SD, range): Altitude: 256 ± 22, 237–281 m; annual rainfall: 521 ± 27, 497–559 mm; annual temperature (max. + min. /2): 22.9 ± 0.3, 22.5–23.1°C (N=4).

Habitat: Not recorded for South Africa.

Food types: No quantitative assessment; DBRU collection records from dung of baboon (1), elephant (1), zebra (1), waterbuck (1).

Temporal activity: Diurnal flight activity in the summer rainy season (Mar.).

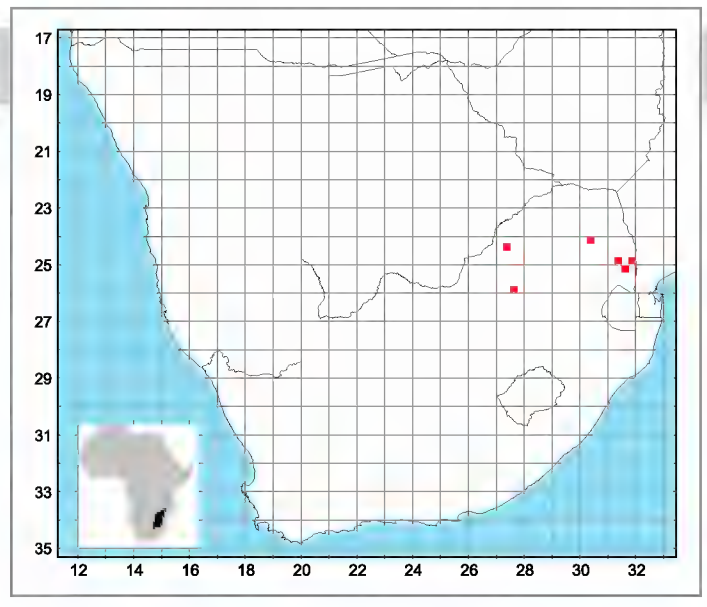
Bioregions South Africa: Centred on Mopane (SVmp) (Savanna Biome).

Assessment rationale: EOO = 253 700 km^2 (assumes unsupported continuous distribution from S to E Africa); widespread, but with probable disjunct distribution; known AOO in NE Africa and NE South Africa much smaller; known distribution in South Africa very restricted, but entirely confined within a national park; therefore, assessed as Least Concern (LC) although somewhat Data Deficient (DD).

Conservation measures: Assuming that a review of the taxonomy validates the identity of the South African population as *G. reichei*, a quantitative survey is required to determine its full EOO, AOO and ecological associations in southern Africa; protected in Kruger National Park.

Gymnopleurus thelwalli

Waterhouse, 1890



No synonyms

Global: DD (see IUCN Red List – DD)

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Lake Nyassa' [environs of Lake Malawi].

Taxonomy: Accepted species; morphologically distant from other southern African taxa.

Distribution: Validated records from Malawi, South Africa; also reported from Zimbabwe, Tanzania; known only as a rarity from scattered savanna localities.

Locality data (mean ± SD, range): Altitude: 617 ± 416, 301–1 382 m; annual rainfall: 661 ± 51, 553–700 mm; annual temperature (max. + min. /2): 21.5 ± 2.4, 17.8–25.9°C (N=7).

Habitat: Not known.

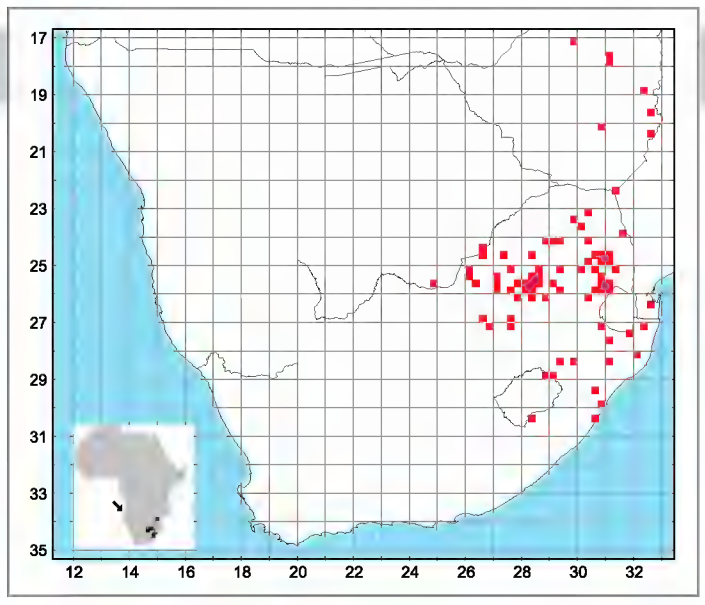
Food types: Not known.

Temporal activity: Diurnal flight activity in the summer rainy season (Dec., Feb.).

Bioregions South Africa: Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 555 105 km^2 (probably underestimated); widespread savanna range, but known by only a few museum specimens, possibly because of specialisation; AOO may or may not be much smaller than EOO; very poorly known both biogeographically and ecologically; assessed as Data Deficient (DD).

Conservation measures: To assess conservation status, quantitative data are required to determine if the AOO would be influenced by ecological specialisation; an ideal focal area would be Skukuza where it has been recorded with greatest frequency in South Africa; this would permit predictions of AOO across its widespread recorded EOO; protected in the S Kruger National Park (South Africa).



Gymnopleurus virens

Erichson, 1843

(see Taxonomy section – all synonyms are errors)
= *Gymnopleurus pumilus* Reiche, 1850
= *Gymnopleurus gibbosus* Roth, 1851
= *Gymnopleurus vanderkelleni* van Lansberge, 1886
= *Gymnopleurus virens* Erichson subsp. *sternalis* Müller, 1942

Global: LC (see IUCN Red List – LC)*

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *G. virens*: 'Angola'; *G. pumilus*: 'Abyssinie' [Ethiopia]; *G. gibbosus*: 'abyssinien' [Ethiopia]; as '*G. van der Kelleni*': 'West Africa' [probably Angola]; subsp. *sternalis*: 'Aethiopia meridionali' [southern Ethiopia].

Taxonomy: Accepted species, but revision is required to correct errors; this mostly iridescent green species, trending to blue in moister and/or cooler situations, has often been confused (e.g. Ferreira 1972) with an E to NE African relative, *G. sericeifrons* Fairmaire, 1887, described from 'Makdischu' [Mogadishu, Somalia]; however, it most strongly resembles the finer-punctate type of *G. virens* Erichson, 1843, described from Angola; all of the cited synonyms are considered to be errors; the Ethiopian types most strongly resemble a more coarsely punctate southern African taxon, which is the species usually cited as *G. virens* (but see account for that species under the name, *G. pumilus*); *G. vanderkelleni* is a misidentified synonym of *G. aenescens* Wiedemann, 1821, or a close relative of that species.

Distribution: Possibly disjunct pattern in moist southern African upland and coastal plain savanna; also marginal in warmer grassland: validated for N South Africa, Mozambique coast, E Botswana, E Zimbabwe, SW Angola (Bié Plateau).

Locality data (mean ± SD, range): Average altitude: 1 089 ± 497, 5–2 274 m; average annual rainfall: 739 ± 141, 383–1 142 mm; average annual temperature (max. + min. /2): 18.5 ± 2.6, 10.6–25.2°C (N=114).

Habitat: On Gauteng bushveld: extreme association with finer-grained soils: sandy clay loam (1 233), deep sand (1), and appreciable bias to open woodland (838) as opposed to grassland (239) or shaded thickets (156); supported by DBRU collection records from sand (3), sandy loam (10), sandy clay loam (3) in grassland/pasture (4), shrubland (4), open woodland (10), forest (1).

Food types: No quantitative assessment; DBRU collection records presumably biased by more commonly sampled dung types: human (2), human/cattle mix (2), elephant (3), cattle (17).

Temporal activity: Diurnal flight activity, primarily in the summer rainy season (Oct. to Mar.); on Gauteng bushveld: greatest activity early in summer rainy season continuing to Mar., declining to low levels in Apr., May, ceasing in June and commencing again in Sept.

Ecoregions Zimbabwe, Mozambique: Southern Miombo Woodlands (AT0719), Maputaland Coastal Forest Mosaic (AT0119).

Bioregions South Africa: Moist S Central Bushveld (SVcb), W and S Lowveld (SVl) (Savanna Biome) along Waterberg and edge of Highveld; warmer N Mesic Highveld Grassland (Gm) and N Sub-Escarpment Grassland (Gs) (Grassland Biome); N Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 267 770 km^2 (probably underestimated); AOO would be smaller, reflecting soil and vegetation bias; probably influenced by woodland clearance, but also found in warmer moist grasslands; widespread in farmland and protected in various nature reserves, assessed as Least Concern (LC); *IUCN Red List entry also includes data for *G. pumilus* Reiche, 1850.

Conservation measures: Assessment of conservation status would be improved by quantitative data on food type associations; protected in Rustenburg and Leeuwfontein nature reserves (South Africa).

TRIBE ONITICELLINI

Kolbe, 1905

Subtribe Drepanocerina van Lansberge, 1875a: As Drepanocérides; Type genus: *Drepanocerus* Kirby, 1828.

Subtribe Oniticellina Kolbe, 1905: As Oniticellini; Type genus: *Oniticellus* Dejean, 1821.

Subtribe Helictopleurina Janssens, 1946: As Helictopleurides; Type genus: *Helictopleurus* d'Orbigny, 1915.

Subtribe Liatongina Philips, 2016: Type genus: *Liatongus* Reitter, 1892.

Subtribe Attavicina Philips, 2016: Type genus: *Attavicinus* Philips & Bell, 2008.

As regards citation of subtribal names in older format, Drepanocerina has precedence over that of Oniticellina. However, at tribal level the name Oniticellini should be maintained as it has been in prevailing long-term usage (Smith 2006). According to Philips (2016), subtribal divisions (van Lansberge 1875a; Kolbe 1905; Janssens 1946) are partially valid owing to monophyly in the Drepanocerina and Madagascar endemic, Helictopleurina. They are partially invalid as regards the Oniticellina, which are paraphyletic. Therefore, Philips (2016) proposes two new subtribes, Attavicina and Liatongina, of which only Liatongina are represented in southern Africa by two species.

Phylogenetic analysis of molecular data for selected taxa suggests monophyly at tribal level (Monaghan et al. 2007) although different analyses of morphological data, together with those for Onthophagini, support either monophyly or polyphyly (Philips 2016). The tribe currently comprises 25 or 26 genera depending on the authority followed. A total of 18 are regional endemics: Afrotropical (10), Oriental (3), Palaearctic (1), Neotropical (1), Jamaica (1) or Madagascar (2). The remainder are shared between regions: **(A)** Afrotropical, Oriental (5: *Eodrepanus* Barbero, Palestrini & Roggero, 2009; *Ixodina* Roth, 1851; *Oniticellus* Dejean, 1821; *Tibiodrepanus* Krikken, 2009; *Tiniocellus* Péringuey, 1901); **(B)** Afrotropical, Oriental Palaearctic (1: *Drepanocerus* Kirby, 1828); **(C)** Afrotropical, Oriental, Palaearctic, Cuba (1: *Euoniticellus* Janssens, 1953); **(D)** Afrotropical, Oriental, Palaearctic, Nearctic (1: but polyphyletic; *Liatongus* Reitter, 1892).

A total of 14 genera and 26 named species are represented in South Africa, Botswana and Namibia (summary below). They are mostly assessed as Least Concern (LC) owing to mostly very wide distributions (EOO > 500 000 km^2 in 20 out of 26 species), often with high abundance. A few are assessed as Data Deficient (DD). A few species (6) are associated with monogastric herbivore dung, but also show widespread ranges.

Subtribe Drepanocerina:

(1) *Afrodrepanus* Krikken, 2009: A single species endemic to SE South African forest and shaded vegetation.

(2) *Cyptochirus* Lesne, 1900: A single species with a disjunct distribution in upland grassland from SE to E Africa; patterned variety in moist savanna requires further examination.

(3) *Drepanocerus* Kirby, 1828: Two species in grassland to savanna; distributed from S to E Africa.

(4) *Eodrepanus* Barbero, Palestrini & Roggero, 2009: Three species in dry to moist savanna and grasslands from SE to E Africa.

(5) *Epidrepanus* Roggero, Barbero & Palestrini, 2015: Probably a single species in South Africa, but possibly two species with combined distributions from SE to E to W Africa.

(6) *Ixodina* Roth, 1851: A single poorly known species distributed from SE to E Africa.

(7) *Latodrepanus* Krikken, 2009: A single species in sandy savannas from S to E to W Africa.

(8) *Paraixodina* Roggero, Palestrini & Barbero, 2015: Two species of monogastic herbivore dung distributed from SE to E African savannas.

(9) *Tibiodrepanus* Krikken, 2009: A single species of moist SE African grasslands distributed from S to E to W Africa.

Subtribe Onticellina:

(10) *Euoniticellus* Janssens, 1953: Five species; two from monogastric herbivore dung distributed from S to E or S to E to W Africa; three other widespread species centred in cool South African grasslands, moist grasslands from SE to E Africa, or various non-forest regions from S to E to W Africa.

(11) *Oniticellus* Dejean, 1821: Four widespread species; one on monogastric herbivore dung distributed from S to E Africa; two species centred on dry or moist savannas from S to E to W Africa; one species centred mostly on cool upland in SE and E central Africa.

(12) *Tiniocellus* Péringuey, 1901: Two species; one endemic to SE savannas; one widespread in savannas from S to E Africa.

(13) *Tragiscus* Klug, 1855: A single species on monogastric herbivore dung in dry to moist savannas; widespread in savannas from S to E Africa.

Subtribe Liatongina:

(14) *Liatongus* Reitter, 1892: A single widespread species, primarily centred in moist grasslands from SE to E Africa; one unidentified forest species in SE South Africa (no species account).

Genus *Afrodrepanus* Krikken, 2009

Type species and designation: *Drepanocerus impressicollis* Boheman, 1857, by original designation.
Synonyms: None.
Last review: Genus created and reviewed by Krikken (2009), morphological phylogeny Roggero et al. (2015).

Afrodrepanus Krikken, 2009, comprises only two species endemic to the Afrotropical region. One species shows a tropical distribution in E and W Africa. The second species has a validated distribution in shaded savanna (thicket) and forest vegetation of NE South Africa.

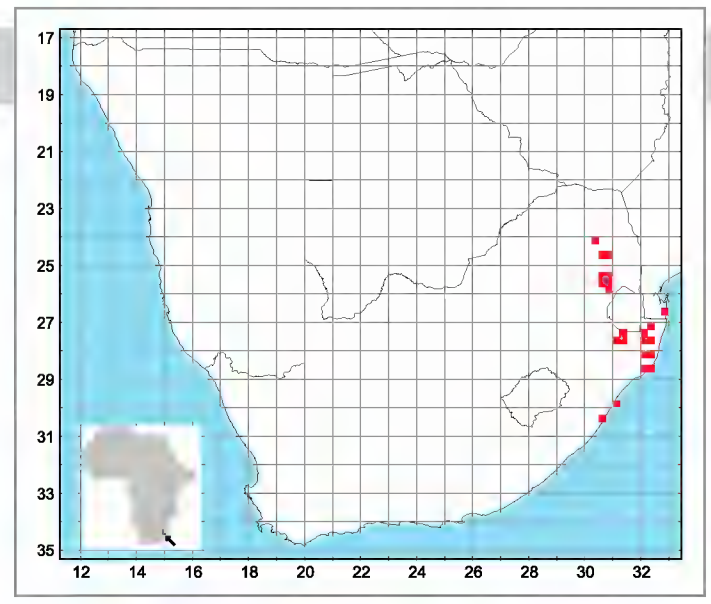
Afrodrepanus impressicollis

(Fahraeus, 1857)

= *Drepanocerus natalensis* Harold, 1859

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: As *Drepanocerus impressicollis*: 'Caffraria meridionali' [S southern Africa]; *D. natalensis*: 'Port Natal' [Durban, KwaZulu-Natal, South Africa].

Taxonomy: Accepted species in the subfamily, Drepanocerina.

Distribution: Mostly lower-altitude, moist, shaded vegetation; NE coast and NE escarpment, South Africa; SE coast Mozambique; citations from Zimbabwe, Tanzania and Kenya require validation in comparison with the tropical *A. marshalli* (Boucomont, 1921).

Locality data (mean ± SD, range): Average altitude: 595 ± 610, 0–1 746 m; average annual rainfall: 875 ± 123, 656–1 094 mm; average annual temperature (max. + min. /2): 19.5 ± 2.6, 14.0–22.4°C (N=32).

Habitat: On sandy loam in Ithala Game Reserve: abundant in dense low-altitude woodland (Ngubu 714 m: 192; Dakaneni 511 m: 621; Combretum woodland 690 m: 228), becoming uncommon at higher altitude (Ntshondwe Forest 975 m: 15) and absent from mid-altitude grassland at 945 m (0); in Wolkberg: present, but uncommon in forest at 901 m (2.65 per pig dung sample); absent from forest and grassland at 1 355–1 397 m (0); on deep sand at Richards Bay: bias to natural dune forest (14.1 per sample) compared to post-mining vegetation succession: grassland < 1–6 yr (0.0), dense/closed canopy woodland 7–21 yr (0.5), open canopy woodland 21–33 yr (0.0); in uMkhuze Game Reserve: possible bias to finer-grained soils: sand (0.0), sand on clay (0.4), sandy clay loam (0.4), clay (0.5).

Food types: In Ithala Game Reserve: very strong bias to omnivore dung (pig: 890) compared to monogastric (horse: 47) and ruminant herbivore dung (cattle: 119).

Temporal activity: Diurnal flight activity, primarily during the summer rainy season (Sept. to May).

Ecoregions Mozambique: Maputaland Coastal Forest Mosaic (AT0119).

Bioregions South Africa: Indian Ocean Coastal Belt Biome (CB); dense bushveld and thicket at SE and W edges, Lowveld (SVl) (Savanna Biome); often in patches of Northern Mistbelt Forest (FOz 4) and Northern Coastal Forest (FOz 7).

Assessment rationale: EOO = 27 860 km²; AOO would be much smaller according to distribution of dense vegetation offering shade across a range that is subject to extensive habitat transformation (0–58%, SVl); however, owing to size of range and protection offered in various reserves, currently assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by stronger quantitative data on soil associations and a survey of dense vegetation patches potentially occupied by *A. impressicollis*; protected in Ithala, uMkhuze and Hluhluwe–iMfolozi game reserves (South Africa), Maputo Elephant Reserve (Mozambique).

Genus *Cyptochirus* Lesne, 1900

Type species and designation: *Onitis ambigua* Kirby, 1828, by monotypy.
Synonyms: = *Drepanochirus* Péringuey, 1901: Type species: *Onitis ambigua* Kirby, 1828, by monotypy.
Last review: Entire genus reviewed by Simonis and Zunino (1980); morphological phylogeny by Roggero et al. (2015).

Cyptochirus Lesne, 1900, was revalidated from synonymy with *Drepanocerus* Kirby, 1828, by Simonis and Zunino (1980). It currently comprises four species endemic to moist savanna and upland grassland of the Afrotropical region where they construct a brood chamber immediately under droppings (Cambefort 1981).

Morphological phylogeny (Roggero et al. 2015) supports the validity of the four very closely related species, but cited biogeographical overlap between species in upland centres in southern Africa, E Africa, E central Africa, NE Africa and W Africa may require further investigation; particularly the claimed occurrence of a second species in South Africa that was described from Ethiopia.

As ranges in body size overlap between all four *Cyptochirus* species (Simonis & Zunino 1980), further investigation should compare specimens of similar body size, e.g. 10 mm long, to ensure claimed specific differences are not related to morphological variation with body size. A molecular phylogeny would also be useful. Here, only one species is considered to occur in upland grassland in South Africa although a light and darker brown patterned 'variety' has been recorded primarily in monogastric herbivore dung in lowland savanna of both South Africa and Zimbabwe.

Cyptochirus ambiguus

(Kirby, 1828)

= *Oniticellus impressus* Castelnau, 1840

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Onitis ambigua*: 'Promontorium Bonae Spei'; *O. impressus*: 'Cap de Bonne-Espérance' [both Cape of Good Hope, South Africa].

Taxonomy: Accepted species in the subfamily Drepanocerina; limited sexual dimorphism (legs); some individuals from NE KwaZulu-Natal and moist Zambezi Valley edge show a dark brown pattern on light brown elytra; taxonomic status of patterned individuals requires assessment; claimed occurrence of *C. trogiformis* (Roth, 1851), in South Africa also requires validation considering it was described from Ethiopia.

Distribution: Moist, warmer parts of Highveld and SE coast of South Africa (red squares; blue square = outlier): South Africa, Eswatini; plus claimed disjunct pattern of occurrence in E/NE African highlands: Tanzania Kenya; further citations from Democratic Republic of the Congo (DRC), Uganda, Ethiopia suggest sympatry with other *Cyptochirus* species, but require validation; patterned individuals: South Africa, Zimbabwe lowland savanna (black squares).

Locality data (mean ± SD, range): Unpatterned: Altitude: 1 046 ± 586, 21–2 286 m; annual rainfall: 775 ± 137, 430–1 047 mm; annual temperature (max. + min. /2): 16.9 ± 2.4, 10.8–22.6°C (N=112); Patterned: Altitude: 328 ± 277, 55–879 m; annual rainfall: 762 ± 107, 649–904 mm; annual temperature (max. + min. /2): 22.1 ± 2.2, 18.4–25.9°C (N=10).

Habitat: No adequate quantitative assessment; at Foggy Valley unpatterned form abundant in natural *Themeda* grasslands (104), fallow crop fields (72) and Kikuyu pasture (94); DBRU collection records from sand (3), sandy loam (18), sandy clay loam (24), clay (6) primarily in grassland/pasture (46), rare in shrubland (1), open woodland (2), forest (1); patterned form on sand (1), sandy loam (1), sandy clay loam (1) in open woodland (3) or thicket (1).

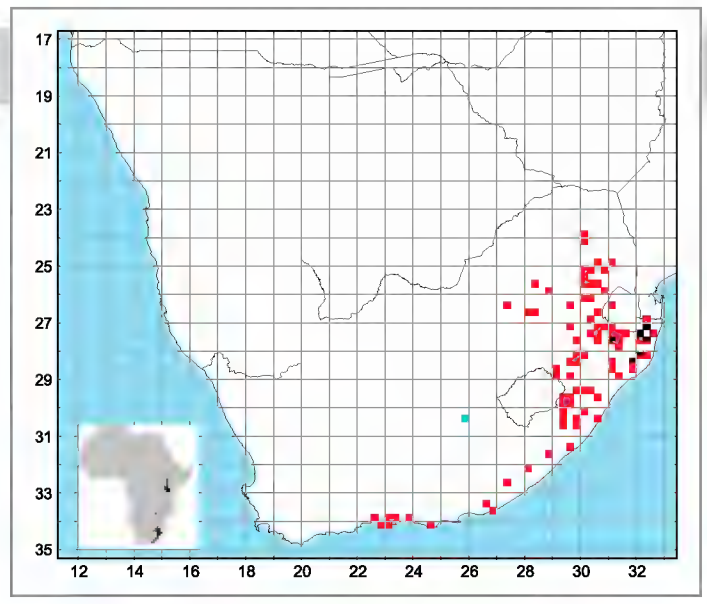
Food types: No quantitative assessment; DBRU collection records for unpatterned form primarily from dung of cattle (53), also elephant (1); patterned form primarily from monogastric dung: rhinoceros (4), elephant (1), wildebeest (1).

Temporal activity: Diurnal flight activity during the summer rainy season (Oct. to May).

Bioregions South Africa: Centred on E Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs) (Grassland Biome), transformed habitats on S coast in Fynbos Biome, marginal along coast in three other biomes; both unpatterned and patterned forms in moist S Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 323 350 km²; even though S and E African unpatterned populations may comprise one or two different species; both are widespread, although not currently known from any highland reserve in South Africa; frequently recorded from cattle dung in both farmed and natural moist grasslands; patterned individuals may comprise a further species with a much smaller AOO as they are apparently associated with the dung of large monogastric herbivores that are primarily restricted to game reserves in moist savanna; assessed as Least Concern (LC).

Conservation measures: A taxonomic revision is required; should patterned individuals deserve species status, a survey to determine their full EOO, AOO and conservation status would be required; furthermore, quantitative ecological data for all populations would improve assessments; patterned form protected in Tembe Elephant Park and Hluhluwe–iMfolozi Game Reserve.



Patterned variety (black squares on map).

Unpatterned variety (red squares on map).

Genus *Drepanocerus* Kirby, 1828

Type species and designation: *Drepanocerus kirbyi* Kirby, 1828, by monotypy.
Synonyms: None.
Last review: Entire genus reviewed by Krikken (2009); morphological phylogeny (Roggero et al. 2015: three Afrotropical species).

Membership of the genus, *Drepanocerus* Kirby, 1828, was reduced to only four species by the revision of Krikken (2009). These comprise three Afrotropical and one Oriental species. Two Afrotropical species occur in the E savanna and upland grasslands of southern Africa with ranges extending into the E tropics. The third species is centred on E Africa.

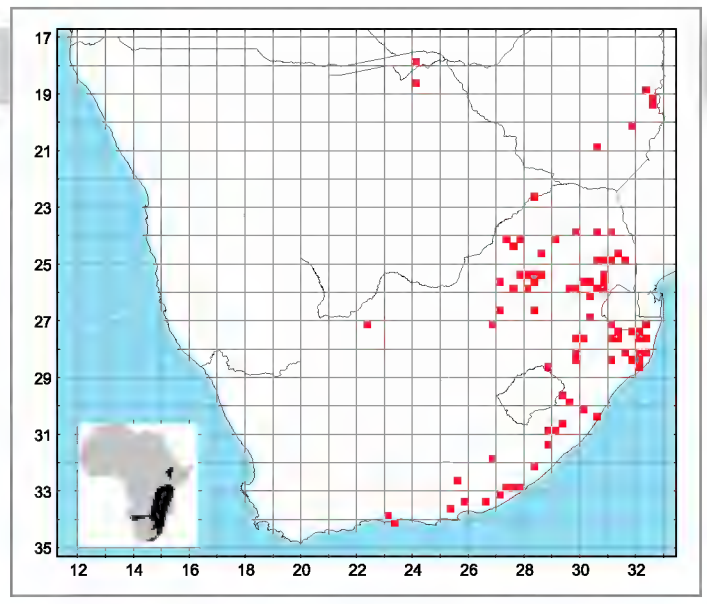
Drepanocerus kirbyi

Kirby, 1828

= *Oniticellus furcifer* Castelnau, 1840

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: As *D. kirbii*: 'Promontorium Bonae Spei'; *O. furcifer*: 'Cap de Bonne-Espérance' [both Cape of Good Hope, South Africa].

Taxonomy: Accepted species in the subfamily, Drepanocerina; sexual dimorphism (head, prothoracic disc), characters varying in prominence with body size.

Distribution: Savanna and grassland from S and S Central to NE Africa: South Africa, N Namibia, N Botswana, Zimbabwe, Mozambique, Tanzania, Kenya; also reported from Angola, Democratic Republic of the Congo (DRC), Rwanda, Ethiopia.

Locality data (mean ± SD, range): Altitude: 883 ± 597 0–3 218 m; annual rainfall: 733 ± 175, 306–1 659 mm; annual temperature (max. + min. /2): 18.4 ± 2.9, 4.8–25.2°C (N=112).

Habitat: Soil generalist with a bias to woody vegetation in Gauteng: deep sand (1 968), sandy clay loam (2 099); grassland (677), open woodland (1 890), shaded thicket (1 500); however, DBRU collection records from sand (10), sandy loam (23), sandy clay loam (10), clay (3) in grassland/pasture (31), shrubland (6), open woodland (7), forest/thicket (2).

Food types: In Gauteng and Phalaborwa: strong bias to dung of ruminant and monogastric herbivores, cattle (307/192), horse/elephant (169/102), pig (24/17); DBRU collection records primarily from cattle dung (48), also elephant (2), horse (1).

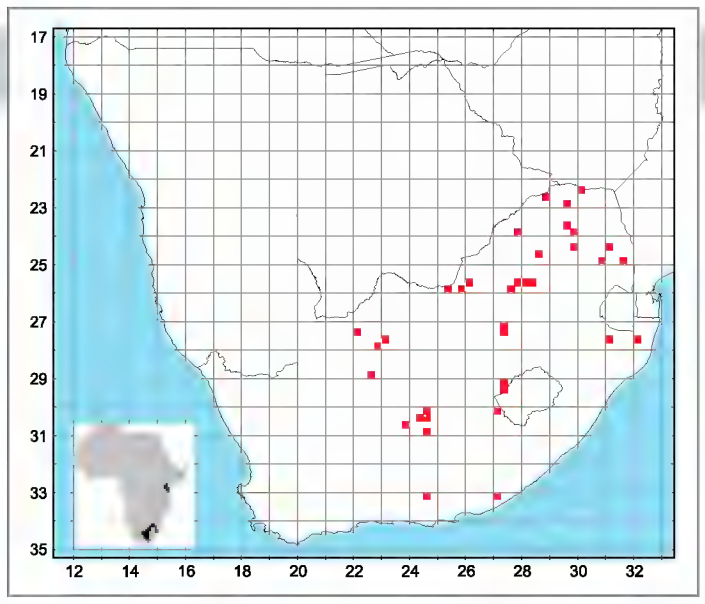
Temporal activity: Diurnal flight activity; in Gauteng: mostly between 10:00–16:00 with peak at midday (12:00–14:00) or mid-afternoon (14:00–16:00); active throughout year with peak activity in summer rainy season (Oct. to May), tailing off in June to low levels in the late dry season; at Phalaborwa: frequency greater in warm sunny conditions soon after heavy rainfall (226) than in hot, dry (69) or warm cloudy conditions (14) following light rainfall.

Ecoregions Namibia, Botswana, Zimbabwe: Zambezian and Mopane Woodlands (AT0725), Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome); E Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs) (Grassland Biome); Indian Ocean Coastal Belt Biome (CB), Albany Thicket Biome (AT), transformed habitats in E coastal part of Fynbos Biome.

Assessment rationale: EOO = 3 526 325 km^2; widespread in both savanna and grassland despite a measured bias to woody habitats; occurs in both farmland and reserves owing to a strong bias to association with dung of both indigenous and domestic herbivores; assessed as Least Concern (LC).

Conservation measures: None recommended; recorded in both farmland and various game reserves including Hluhluwe–iMfolozi, uMkhuze, Ithala (South Africa).



Drepanocerus patrizii

(Boucomont, 1923a)

= *Drepanocerus arthuri* Boucomont, 1936

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Cyptochirus patrizii*: 'N. Kenia' [N Kenya]; *D. arthuri*: 'Afrique orientale anglaise: Embaki' [Tanzania: Lake Embaki in Ngorongoro Conservation Area].

Taxonomy: Accepted species in the subfamily, Drepanocerina; sexual dimorphism (head), characters varying in prominence with body size.

Distribution: Disjunct occurrence in dry savanna and grasslands of S and E Africa separated by moister climate: South Africa, Kenya, Tanzania; also reported from Namibia, Zimbabwe.

Locality data (mean ± SD, range): Altitude: 1 129 ± 409, 93–1 759 m; annual rainfall: 536 ± 189, 254–975 mm; annual temperature (max. + min. /2): 18.0 ± 2.5, 13.9–23.4°C (N=41).

Habitat: In Gauteng bushveld: relatively generalist with slight bias to finer-grained soils and more open vegetation: deep sand (333), sandy clay loam (594); grassland (320), open woodland (482), shaded thickets (111); largely supported by DBRU collection records: sand (1), sandy loam (16), sandy clay loam (3), clay (2) in grassland/pasture (10), shrubland (6), open woodland (5).

Food types: In Gauteng and Phalaborwa: equal bias to herbivore dung types: cattle (14/3), horse/elephant (14/3); absent from omnivore dung: pig (0/0); DBRU collection records from dung of cattle (19), horse (1), donkey (1).

Temporal activity: Diurnal flight activity; in Gauteng: mostly between 10:00 and 16:00 with a mid-summer peak at midday (12:00–14:00) or early/late summer peak in mid-afternoon (14:00–16:00); recorded throughout the year except late dry season (Aug., Sept.), but most abundant early to mid-rainy season (Oct. to Feb.), tailing off into late summer and the dry season.

Bioregions South Africa: Central Bushveld (SVcb), Mopane (SVl), Lowveld (SVl), Eastern Kalahari Bushveld (SVk) (Savanna Biome); Dry Highveld Grassland (Gh) (Grassland Biome); E Upper Karoo (NKu) (Nama Karoo Biome); Albany Thicket Biome (AT); margins of two other bioregions.

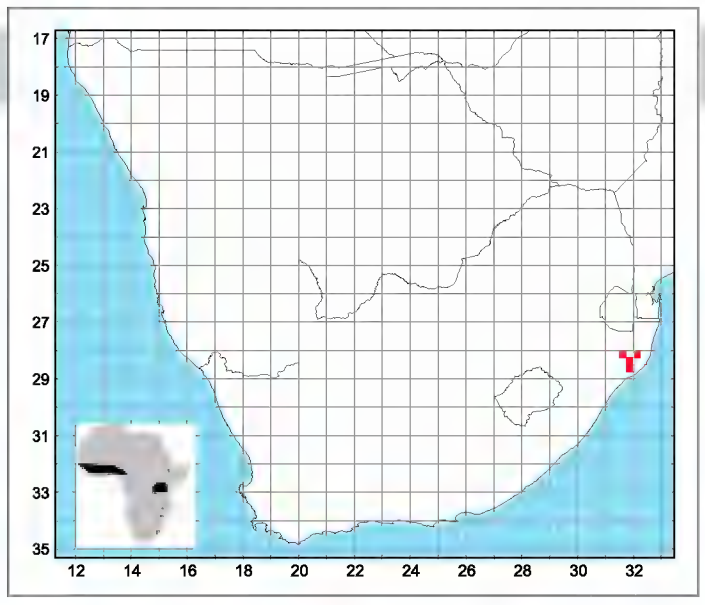
Assessment rationale: EOO = 503 040 km^2; widespread under drier climate in both farmland and game reserves owing to fairly generalist habitat associations and association with both ruminant and monogastic herbivore dung; thus assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by a distributional survey to confirm the disjunct EOO; protected in Kruger National Park, Ithala Game Reserve (South Africa), Amboseli and Marsabit game reserves (Kenya).

Genus *Eodrepanus* Barbero, Palestrini & Roggero, 2009a

Type species and designation: *Drepanocerus parallelus* Raffray, 1877, by original designation.
Synonyms: None.
Last review: Entire genus created and reviewed by Barbero et al. (2009a); morphological phylogeny (Roggero et al. 2015).

Eodrepanus Barbero, Palestrini & Roggero, 2009a was created to accommodate nine species: eight of them extant, primarily from the savannas and grasslands of the Afrotropical (5) and Oriental regions (3), one of them extinct, known as a fossil from the Palaearctic region (England). All three of the species recorded in southern Africa are only known from N Botswana and (primarily) E South Africa where two are found in E savanna and one in forest, savanna and grassland. All three species also range into the E tropics.



Eodrepanus bechynei

(Janssens, 1953)

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Drepanocerus bechynei*: 'Abyssinie: lac Daka (Type)' [Holotype: Lake Daka, Ethiopia].

Taxonomy: Accepted species in the subfamily, Drepanocerina.

Distribution: Apparently disjunct, high rainfall, lowland and upland tropical pattern along E seaboard from (1) NE coastal hills of South Africa to uplands of NE Africa (South Africa, Mozambique, E Democratic Republic of the Congo (DRC), Rwanda, Burundi, Tanzania, Zambia, Kenya, Uganda, Ethiopia) and (2) lowland West Africa (Gambia, Guinea (Conakry), Côte d'Ivoire, Ghana, Benin, Burkina Faso, Niger, Nigeria, Cameroon); also cited from Senegal, Guinea (Bissau).

Locality data (mean ± SD, range): Altitude: 421 ± 556, 144–1 464 m; annual rainfall: 1 021 ± 315, 826–1 659 mm; annual temperature (max. + min. /2): 20.2 ± 1.5, 17.2–21.1°C (N=6).

Habitat: No quantitative assessment; limited DBRU collection records from deep sand (1), sandy clay loam (1), clay (1) in pasture/grassland (2).

Food types: No quantitative assessment; limited DBRU collection records from dung of cattle (1), buffalo (1), rhinoceros (1).

Temporal activity: Diurnal flight activity primarily in the summer rainy season (Aug., Nov., Mar., Apr.).

Bioregions South Africa: Moist S Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 2 080 435 km^2 (gross estimate); poorly known ecologically; apparently restricted to a very small, disjunct, range in southern Africa, but widespread in parts of the wet tropics; known range in South Africa mostly protected; therefore assessed as Least Concern (LC) although essentially Data Deficient (DD).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; protected in Hluhluwe–iMfolozi Game Reserve (South Africa).

Eodrepanus fastiditus

(Péringuey, 1901)

No synonyms

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Drepanocerus fastiditus*; 'Natal (Frere, Durban, Estcourt)' [KwaZulu-Natal, South Africa].

Taxonomy: Accepted species in the subfamily, Drepanocerina; limited sexual dimorphism (prothoracic disc, elytra).

Distribution: Moist coastal and upland areas along E seaboard from S to NE Africa: South Africa, Zimbabwe, Mozambique, E Democratic Republic of the Congo (DRC), Burundi, Kenya, Uganda, Ethiopia, Eritrea; also cited from Rwanda, Tanzania; record from Guinea (Bissau) requires validation; southern African disjunctions probably a mix of collection artefacts and unsuitable habitat or climate.

Locality data (mean ± SD, range): Altitude: 941 ± 511, 1–1 782 m; annual rainfall: 759 ± 209, 240–1 659 mm; annual temperature (max. + min. /2): 18.5 ± 2.3, 13.8–25.2°C (N=56).

Habitat: In Gauteng bushveld: bias to sandy clay loam (95) compared to deep sand (24) and bias to open vegetation, grassland (69), open woodland (46), shaded thicket (4); largely supported by DBRU collection records: bias to finer-grained soils, deep sand (4), sandy loam (4), sandy clay loam (3), clay (2) in grassland/pasture (8), open woodland (4), forest (1), also fallow crop fields (2).

Food types: At Phalaborwa: strong bias to monogastric herbivore dung (elephant: 13) compared to ruminant herbivore (cattle: 2) and omnivore dung (0); DBRU collection records primarily from dung of cattle (9), horse (2), elephant (1), human/cattle mix (1).

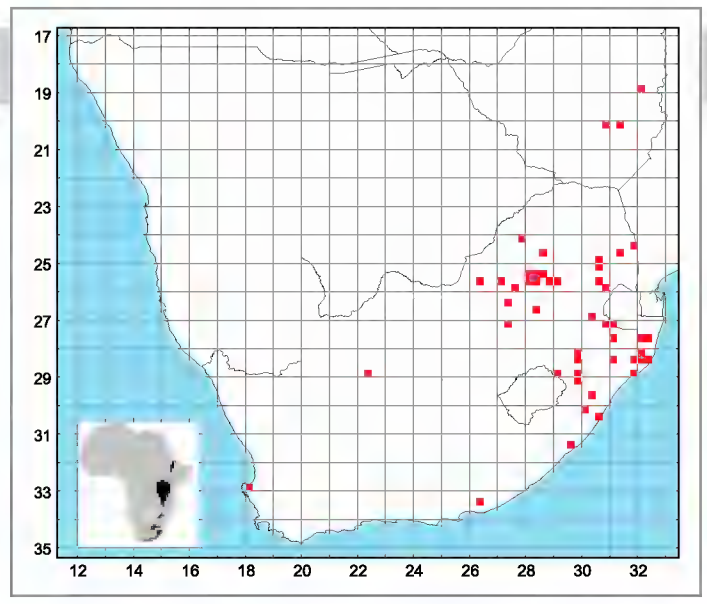
Temporal activity: Diurnal flight activity, primarily during the summer rainy season (Aug. to Apr.); at Phalaborwa: primarily active in hot sunny weather (13), few in warm sunny weather soon after heavy rainfall (2), absent in warm cloudy weather following light rainfall (0).

Ecoregions Zimbabwe: Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Biomes: primarily straddling edges of Indian Ocean Coastal Belt Biome (CB) to Savanna (SV) and Savanna to Grassland (G); Bioregions: Central Bushveld (SVcb), Lowveld (SVl), Sub-Escarpment Savanna (SVs), Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs); marginal in three other bioregions.

Assessment rationale: EOO = 1 517 320 km² (gross estimate); extremely widespread in open vegetation along E seaboard of Africa so soil and climatic bias would not be a threat; however, bias to monogastric herbivore dung would have implications for population density outside of reserves; even so, assessed as Least Concen (LC).

Conservation measures: None recommended owing to widespread occurrence; protected in Leeuwfontein and Tswaing nature reserves, Hluhluwe–iMfolozi Game Reserve (South Africa).



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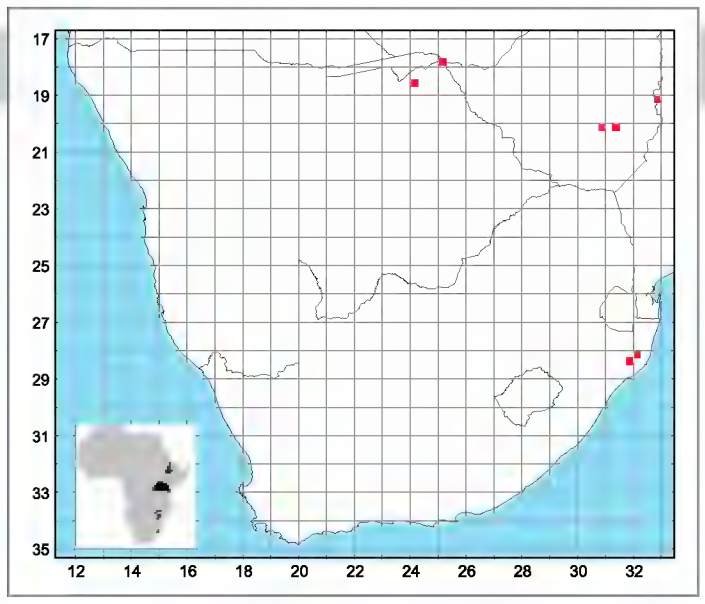


Eodrepanus parallelus

(Raffray, 1877)

No synonyms

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Drepanocerus*? *parallelus*: 'Abyssinie: Province de Tembiène' [Tembien Province, Ethiopia].

Taxonomy: Accepted species in the subfamily, Drepanocerina.

Distribution: Apparent disjunct pattern, primarily in moist savanna along E seaboard from uplands of NE Africa to NE lowlands of South Africa: Eritrea, Ethiopia, Uganda, Kenya, Tanzania, E Democratic Republic of the Congo, Rwanda, Burundi, Malawi, Zambia, Zimbabwe, Mozambique, Botswana, South Africa.

Locality data (mean ± SD, range): Altitude: 754 ± 381, 144–1 108 m; annual rainfall: 755 ± 122, 589–904 mm; annual temperature (max. + min. /2): 21.0 ± 1.8, 19.0–24.4°C (N=8).

Habitat: No quantitative assessment; limited DBRU collection records from sand (2), sandy clay loam (1) in shrubland (1), woodland (1), fallow crop field (1).

Food types: No quantitative assessment; limited DBRU collection records from dung of cattle (2), buffalo (1), rhinoceros (1).

Temporal activity: Diurnal flight activity primarily in the summer rainy season (Aug., Jan., Apr.).

Ecoregions Botswana, Zimbabwe: Southern Miombo Woodlands (AT0719), Zambezian and Mopane Woodlands (AT0725).

Bioregions South Africa: Moist S Lowveld (SVl) (Savanna Biome).

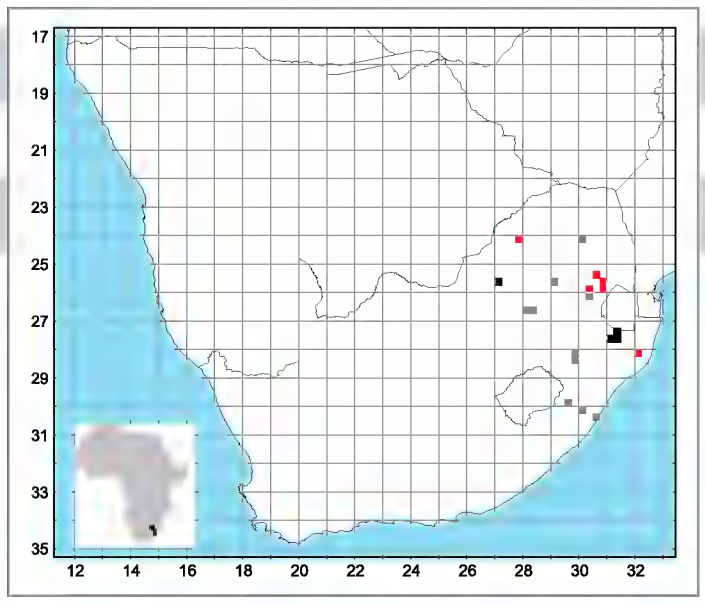
Assessment rationale: EOO = 797 475 km^2 (gross estimate); poorly known ecologically; patchy records from moist savanna of southern Africa, but widespread in parts of the tropics; known range in South Africa mostly protected; therefore, assessed as Least Concern (LC) although essentially Data Deficient (DD).

Conservation measures: Assessment of conservation status would be improved by a quantitative data on ecological associations; protected in Hluhluwe–iMfolozi Game Reserve (South Africa), Chobe National Park (Botswana), Lake Mutirikwe Game Reserve (Zimbabwe).

Genus *Epidrepanus* Roggero, Barbero & Palestrini, 2015

Type species and designation: *Oniticellus caelatus* Gerstaecker, 1871, by original designation.
Synonyms: None.
Last review: Genus created and reviewed with a morphological phylogeny by Roggero et al. (2015).

Epidrepanus Roggero, Barbero & Palestrini, 2015 was created to accommodate three Afrotropical species previously included in the genus, *Latodrepanus* Krikken, 2009. Two species have been recorded in South African uplands. However, these were described from the same type locality in Tanzania and there seems to be much confusion in their identification.



Epidrepanus caelatus

(Gerstaecker, 1871)

Epidrepanus pulvinarius

(Balthasar, 1963c)

No synonyms

Global: DD

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Oniticellus caelatus*: 'Aruscha'; as *Drepanocerus pulvinarius*: 'Ost-Afrika, Tanganjika, Aruscha' [both Arusha, N Tanzania].

Taxonomy: Both accepted species in the subfamily, Drepanocerina; however, each described from the same type locality from only a single unsexed (*E. caelatus*) or a single male specimen (*E. pulvinarius*); material from South African museums variously identified as *E. caelatus* or *E. pulvinarius*, but seems confused.

Distribution: In South Africa: *Epidrepanus* species are centred along the Waterberg, N edge of Highveld Grassland, and edge of NE escarpment; they are primarily recorded in moist open woodland on E coastal hills and in Highveld valleys; also widespread, but rare, across Highveld Grassland; on the map *Epidrepanus* individuals are identified as *E. caelatus* (red squares), *E. pulvinarius* (black squares), or are unidentified to species level (grey squares); Roggero et al. (2017) cite *E. pulvinarius* only from the SE coast and *E. caelatus* primarily from the Highveld and NE coast; across Africa *E. pulvinarius* is cited from Kenya, Tanzania and South Africa (Roggero et al. 2017); *E. caelatus* is cited from Democratic Republic of the Congo, Tanzania, Kenya, Ethiopia, Guinea (or in all seven regions defined from southern to E to W Africa) (Roggero et al. 2015).

Locality data (mean ± SD, range): Altitude: 1 199 ± 408, 273–1 824 m; annual rainfall: 786 ± 117, 576–1 157 mm; annual temperature (max. + min. /2): 17.2 ± 1.8, 14.6–20.5°C (N=24).

Habitat: No adequate quantitative assessment; on finer-grained soils at Suikerbosrand Nature Reserve: only in open woodland (26 at 1 665 m) not Highveld Grassland (0 at 1 662 m) or montane grassland (0 at 1 910 m); on finer-grained soils at Ithala Game Reserve: primarily in shaded woodland at Dakaneni (602 at 472 m), dense shrubland at Ngubu (458 at 706 m) and open Combretum woodland (235 at 711 m), rare in Highveld Grassland (1 at 1 325 m).

Food types: In Ithala Game Reserve: abundant on monogastric herbivore, ruminant herbivore and omnivore dung (horse: 546; cattle: 349; pig: 400).

Temporal activity: Diurnal flight activity primarily in the summer rainy season (Oct. to Feb.).

Bioregions South Africa: Primarily straddling edges of Savanna and Grassland biomes; Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome); N and E edges: both Mesic Highveld Grassland (Gm) and Sub-Escarpment Grassland (Gs) (Grassland Biome).

Assessment rationale: EOO = 160 840 km^2 (range in South Africa); taxonomy unclear, possibly confused; ecological data related to *E. pulvinarius* at Ithala and *Epidrepanus* sp. at Suikerbosrand; both data sets suggest population density would be influenced by clearance of woodland; assessed as Data Deficient (DD) because of taxonomic uncertainty.

Conservation measures: It seems that further taxonomic revision is required to adequately assess the conservation status of *Epidrepanus* species in South Africa; however, ecological data suggest preservation of moist woodland is a requirement for conservation of the species; protected in Suikerbosrand Nature Reserve and Ithala Game Reserve (see above).

Genus *Euoniticellus* Janssens, 1953

Type species and designation: *Scarabaeus fulvus* Goeze, 1777, by original designation.
Synonyms: None.
Last review: Genus created and reviewed by Janssens (1953); new species added by Cambefort and Mauchamps (1980), Cambefort (1983), Biswas and Chatterjee (1985, cited as *Oniticellus*), Masumoto (1987) and by Cambefort (1996a) with a phylogeny of all but the Biswas and Chatterjee species.

Euoniticellus Janssens, 1953, separates groups of larger-bodied tunnelling species and smaller-bodied species of unknown habits from the genus *Oniticellus* Dejean, 1821, which now contains only species showing pad-dwelling, endocoprid breeding habits. The Biswas and Chatterjee species from N India were not included in the phylogeny of Cambefort (1996a). Two of these N Indian species are stated to be close to *E. pallipes* (Fabricius, 1781) and *E. pallens* (Olivier, 1789), both of which have also been recorded in N India.

Euoniticellus shows a distribution in Afro-Eurasia with one species isolated on the Caribbean island of Cuba. It comprises a total of 19 or 21 species represented in the Afrotropical (14), Oriental (1 +?2) and Palaearctic regions (2), with one further species shared between the Afrotropical, W Oriental and S Palaearctic regions.

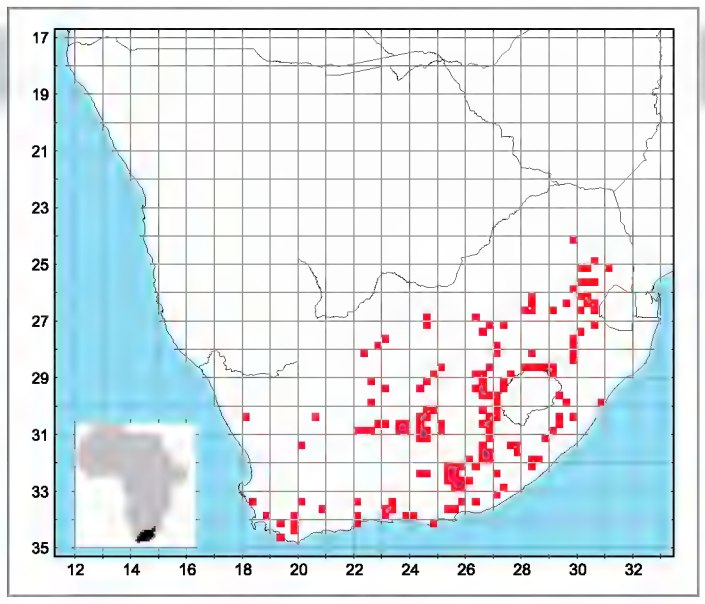
Phylogeny (Cambefort, 1996a) splits the genus into eight more basally derived, smaller-bodied species and 11 more terminally derived, larger-bodied species, which include *E. pallens* and *E. pallipes*. Further study is required to determine the evolutionary, ecological and taxonomic implications of this topology, if any.

In South Africa, Botswana and Namibia, *Euoniticellus* is represented by four larger-bodied and one smaller-bodied species.

Smaller-bodied: One E savanna species associated with elephant dung with a range extending into the E tropics.

Larger-bodied: Four species; one with a savanna distribution and widespead into tropical savanna on elephant dung; three species more frequently recorded on dung of large ruminant herbivores; one widespread thoughout southern Africa and all savanna S of the Sahara; one centred in the S Cape, moist SE savanna and moist N Highveld Grassland with additional occurrence range on E tropical highlands; the third centred on Highveld Grassland, Upper Karoo and the S Cape of South Africa.

The three most terminally derived species showing ruminant dung bias are assessed as Least Concern (LC) as they are widespread and abundant. Those more basally derived species showing elephant dung associations are assessed as Data Deficient (DD).



Euoniticellus africanus

(Harold, 1873)

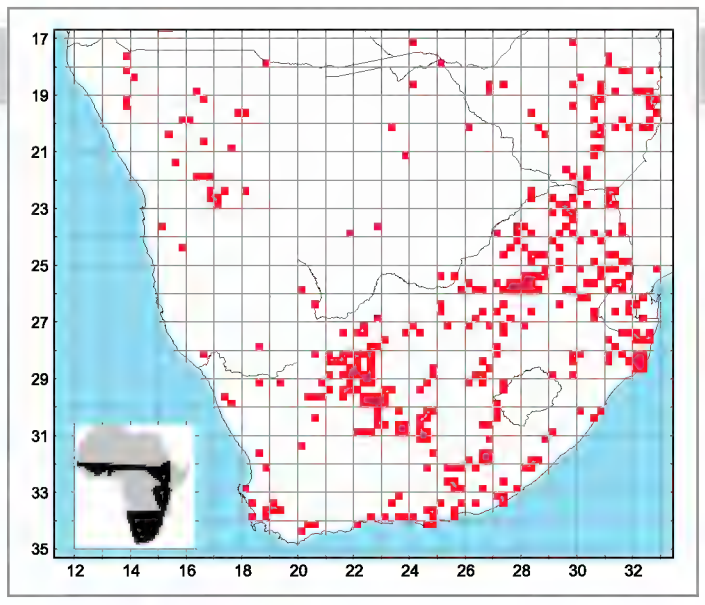
No synonyms

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Oniticellus africanus*: 'Cap bon. spei; Bloemfontein' [South Africa: Cape of Good Hope; Free State].
Taxonomy: Accepted species; limited sexual dimorphism (head).
Distribution: Cool Highveld, Upper Karoo, and SE to S lowlands of South Africa; also reported from Lesotho.
Locality data (mean ± SD, range): Altitude: 1 218 ± 473, 8–2 700 m; annual rainfall: 518 ± 201, 118–1 101 mm; annual temperature (max. + min. /2): 15.8 ± 1.6, 8.0–20.8°C (N=215).
Habitat: No adequate quantitative assessment; in Western Cape: strong bias to transformed pasture habitats (Geelbek: 46, Groote Post: 532, Oranjefontein: 180, Waylands: 454) as opposed to natural shrubland (Geelbek: 1, Modderrivier: 6, Pampoenvlei (sandy loam): 8, Pampoenvlei (sand): 37); DBRU collection records suggest a possible bias to finer-grained soils: sand (17), sandy loam (33), sandy clay loam (50), clay (2) in open vegetation: grassland/pasture (57), scrub (8), open woodland (6), fallow crop fields (4).
Food types: No quantitative assessment; DBRU collection records from dung of cattle (136), buffalo (3), horse (2), zebra (2).
Temporal activity: Diurnal flight activity in spring, summer and autumn across the winter, bimodal (spring, autumn peaks), late summer and mid-summer rainfall regions (Aug. to May).
Bioregions South Africa: Dry Highveld Grassland (Gh), Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs) (Grassland Biome); Eastern Kalahari Bushveld (SVk) (Savanna Biome); Upper Nama Karoo (NKu) (Nama Karoo Biome); Albany Thicket Biome (AT), transformed habitats of Fynbos Biome in S of Western and Eastern Cape; marginal in four other bioregions
Assessment rationale: EOO = 677 390 km²; few known records from protected areas; however, widespread in farmland in South Africa where it is readily attracted to the dung of farm livestock, especially that of cattle; although transformation is extensive in the moister parts of its range (Gh, 4–63%; Gm, 6–69%; Gs, 2–50%); not currently considered threatened; therefore, assessed as Least Concern (LC).
Conservation measures: Quantitative data on ecological associations would improve the assessment of conservation status, particularly, effects of pasture improvement; however, records from transformed habitats in the Fynbos Biome and from fallow crop fields suggest some tolerance of habitat modification; protected in Addo Elephant National Park.

Euoniticellus intermedius



= *Oniticellus pallens* Olivier, 1789, *sensu* Castelnau, 1840
= *Oniticellus clavatus* Roth, 1851
= *Oniticellus speciosus* Costa, 1853
= *Oniticellus nasicornis* Reiche, 1849, *sensu* Péringuey, 1901

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Oniticellus intermedius*: 'Cap de Bonne-Espérance, d'Abyssinie et d'Algérie' [Cape of Good Hope, South Africa; Ethiopia; Algeria]; *O. pallens sensu* Castelnau: 'Sénégal' [Senegal]; *O. clavatus*: Not stated; *O. speciosus* 'Calabrie' [Calabria, S Italy; synonymy requires validation]; *O. nasicornis sensu* Péringuey: 'Cape Colony (Worcester, Knysna, Queen's Town, Kimberley, Graham's Town, Uitenhage, Albert), Natal (Durban, Maritzburg), Transvaal (Potchefstroom, Klerksdorp), Lower Rhodesia (Buluwayo, Enkeldoorn)' [South Africa, Zimbabwe].

Taxonomy: Accepted species; clear sexual dimorphism (head, prothoracic disc), prominence of characters varies with body size.

Distribution: Distributed throughout savannas of S, E, and W Africa with a bias to drier climate; cited from at least 25 sub-Saharan countries; also reported from N Africa (Algeria), Arabia, and as a rarity in S Italy (requires validation); introduced into Australia and USA; dispersed into central America (Mexico, Nicaragua, Costa Rica).

Locality data (mean ± SD, range): Altitude: 967 ± 459, 0–2 286 m; annual rainfall: 507 ± 248, 34–1 659 mm; annual temperature (max. + min. /2): 18.7 ± 2.3, 10.6–25.2°C (N=580).

Habitat: In Gauteng bushveld: no particular soil bias, deep sand (3 676), sandy clay loam (4 464), but much more abundant in grassland (3 429) or open woodland (4 165) as opposed to shaded thickets (546); in Western Cape: strong bias to transformed pasture habitats (Geelbek: 34, Groote Post: 656, Oranjefontein: 364, Waylands: 936) as opposed to natural shrubland (Geelbek: 3, Modderrivier: 29, Pampoenvlei (sandy loam): 21, Pampoenvlei (sand): 106); supported by DBRU collection records from sand (72), sandy loam (56), sandy clay loam (75), clay (13) in grassland/pasture (98), scrub/shrubland (31), open woodland (55), forest/thicket (2); also fallow crop fields (14).

Food types: In Gauteng bushveld: strong bias to dung of pad-dropping ruminant herbivores: cattle (306), horse (46), pig (3), carrion (0); similar bias at Phalaborwa: cattle (1 049), elephant (115), pig (23); DBRU collection records primarily from dung of cattle (255); also, buffalo (13), elephant (4), horse (4), rhinoceros (3), donkey (1), zebra (1), human/cattle or buffalo mixed bait (6), baboon (1).

Temporal activity: Diurnal flight activity peaking at midday (12:00–14:00); in both Gauteng bushveld (summer rainfall) and Western Cape (winter rainfall): active throughout entire year showing greatest abundance in summer, whether dry or wet; at Phalaborwa: frequency much greater in warm sunny conditions soon after heavy rainfall (951) than in warm cloudy conditions following light rainfall (30) or hot, dry conditions (157).

Ecoregions Namibia, Botswana, Zimbabwe: Recorded from most ecoregions of Namibia and Botswana (see summary tables for ecoregions), also Southern Miombo Woodlands (AT0719) in Zimbabwe.

Bioregions South Africa: Recorded from all biomes (Savanna (SV), Grassland (G), Nama Karoo (NK), Succulent Karoo (SK), Indian

Euoniticellus intermedius (continued)

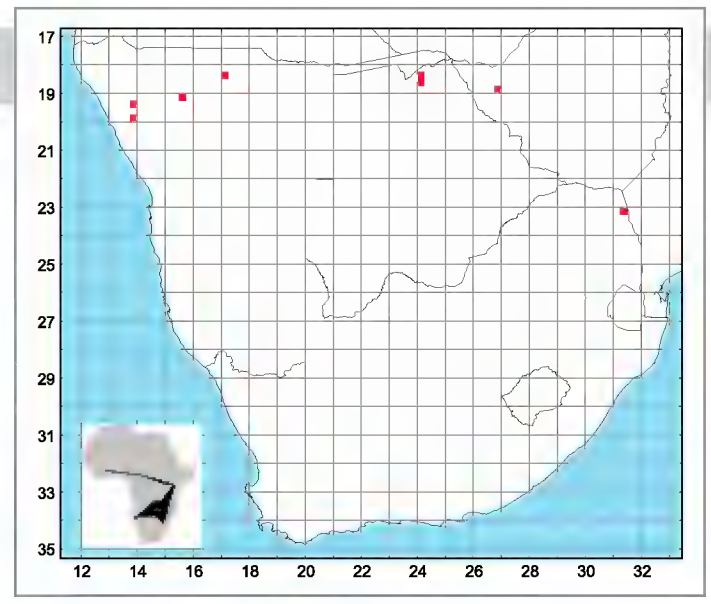
Ocean Coastal Belt (CB), Albany Thicket (AT), Fynbos (F)) and most bioregions, but biased to warmer, drier areas; rare or absent from cooler wetter parts of Highveld.

Assessment rationale: EOO = 9 060 360 km^2 (underestimated sub-Saharan range); open habitat generalist, tolerant of habitat modification; exceptionally widespread throughout African savannas into the Palaearctic region; widely recorded in reserves with further populations resulting from introductions into the Americas and Australia; assessed as Least Concern (LC).

Conservation measures: None recommended; adaptable with a bias to dung pads of ruminant herbivores that are abundant in both farmed areas and game reserves such as Kruger National Park (South Africa).

Euoniticellus kawanus

(Janssens, 1939b)



No synonyms

Global: DD (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Forêt de Kawa, Lac Albert' [not traced; presumably E Democratic Republic of the Congo (DRC)].

Taxonomy: Accepted species, but this savanna-centred species should be validated by comparison with the forest-collected type.

Distribution: Widespread, but patchy occurrence in dry savanna due to dung type specialisation; recorded from S to E to W Africa: South Africa, Namibia, Botswana, Zimbabwe, Democratic Republic of the Congo (DRC), Kenya, Côte d'Ivoire.

Locality data (mean ± SD, range): Altitude: 968 ± 299, 274–1 110 m; annual rainfall: 444 ± 154, 209–608 mm; annual temperature (max. + min. /2): 20.6 ± 2.9, 15.7–23.6°C (N=8).

Habitat: No quantitative data; limited DBRU collection records from sand (1) or sandy loam (3), only in open woodland (3).

Food types: No adequate quantitative data; in Botswana: recorded on elephant (2) and pig dung (1); DBRU collection records from elephant (4) and zebra (1) dung.

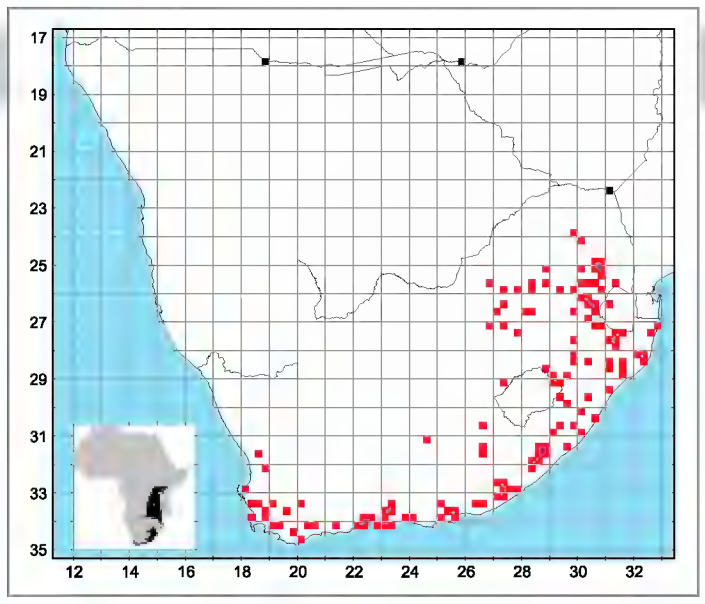
Temporal activity: Diurnal flight activity during the summer rainy season (Nov. to Apr.).

Ecoregions Namibia, Botswana, Zimbabwe: Zambezian and Mopane Woodlands (AT0725), Angolan Mopane Woodlands (AT0702), Namibian Savanna Woodlands (AT1316); margins of one other ecoregion.

Bioregions South Africa: Mopane (SVmp) (Savanna Biome).

Assessment rationale: EOO = 2 691 645 km²; widespread, but infrequently recorded in low numbers suggesting low population density; most available records with ecological data (12) recorded from monogastric herbivore dung; thus AOO would be influenced by the range contraction experienced by these taxa all over Africa with most records from game reserves; ecological data too limited to clearly determine if AOO is further influenced by any habitat bias; assessed as Data Deficient (DD).

Conservation measures: Quantitative data on ecological associations is required to assess conservation status; however, limited observations suggest conservation status would be dependent on the continuing protection of large monogastric herbivores; protected in various national parks and game reserves, including Kruger (South Africa), Hwange (Zimbabwe), Chobe (Botswana), Etosha (Namibia), Meru (Kenya).



Euoniticellus triangulatus

(Harold, 1873)

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Oniticellus triangulatus*: 'Africa australis' [southern Africa].

Taxonomy: Accepted species; limited sexual dimorphism (head).

Distribution: Bias to cool, moist grasslands and transformed pastures from the S and SE coast plus moist Highveld of South Africa to uplands of E Africa (E African DBRU records mostly above 1 400 m: n=28/32; with bias to pasture/grass: n=20/33): South Africa, Namibia, Zimbabwe, Tanzania, Kenya, Eritrea; also reported from Angola, Democratic Republic of the Congo (DRC), Mozambique; W African occurrence requires validation: Guinea, Benin; southern African outliers (black squares) possibly in shade.

Locality data (mean ± SD, range): Altitude: 887 ± 660, 0–3 218 m; annual rainfall: 673 ± 206, 166–1 101 mm; annual temperature (max. + min. /2): 16.9 ± 2.6, 4.8–24.4°C (N=178).

Habitat: No adequate quantitative assessment; in Western Cape: strong bias to cool transformed pasture habitats as opposed to natural shrubland; cool Cape Peninsula (Kikuyu grass pasture on Bonne Attente: 4 478 vs shrubland of Cape of Good Hope Nature Reserve: 2); warmer Darling Hills pasture (Groote Post: 1 229, Oranjefontein: 722, Waylands: 1 394) vs shrubland of adjacent coastline (Modderrivier: 29, Pampoenvlei (sandy loam): 18, Pampoenvlei (sand): 184); DBRU collection records from sand (10), sandy loam (26), sandy clay loam (27), clay (3) with bias to grassland/pasture (53) rather than shrubland (4) or open woodland (3); also fallow crop fields (6).

Food types: No quantitative assessment; DBRU collection records primarily from dung of cattle (90); also buffalo (1), horse (3).

Temporal activity: Diurnal flight activity throughout entire year over entire South African range; to the N: greatest frequency of DBRU records in summer rainy season (Oct. to May); similar to the SW in the Western Cape winter rainfall region: greatest abundance in moist late spring throughout the dry summer till moist autumn (Sept. to May).

Bioregions South Africa: Warmer parts of Grassland Biome: N and E Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs); Indian Ocean Coastal Belt Biome (CB); transformed habitats along S coast in Albany Thicket (AT) and Fynbos Biomes; also margins of Savanna and Nama Karoo Biomes.

Assessment rationale: EOO = 2 234 985 km^2 (underestimated, also recorded in Eritrea); AOO would be somewhat smaller, fragmented, and restricted to grassy highlands and cool dry (to the S) or wet coastal regions (to the N); recorded from few protected areas; however, widespread in farmland where it is readily attracted to cattle dung in natural grassland, habitats transformed to pasture, even fallow crop fields; assessed as Least Concern (LC).

Conservation measures: Quantitative data on ecological associations would improve the assessment of conservation status; protected in Bontebok National Park.

Euoniticellus zumpti

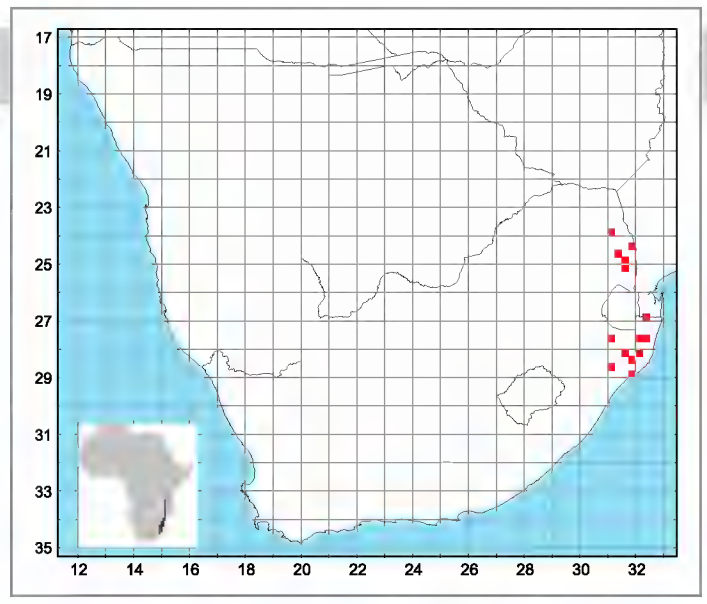
Janssens, 1953

No synonyms

Global: DD

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Hluhluewe, Zululand' [presumably Hluhluwe Game Reserve, KwaZulu-Natal, South Africa].
Taxonomy: Accepted species.
Distribution: Moist to dry lowland savanna from SE to E Africa: South Africa, Mozambique, Kenya; also cited from Tanzania.
Locality data (mean ± SD, range): Altitude: 310 ± 314, 19–1 126 m; annual rainfall: 778 ± 162, 539–1 136 mm; annual temperature (max. + min. /2): 21.4 ± 1.9, 16.8–25.2°C (N=15).
Habitat: No quantitative assessment; observed on deep sand and finer-grained soils; limited DBRU collection records from sand (1) in open woodland (2).
Food types: At Phalaborwa: sampled to dung of elephant (5), pig (1), but not cattle (0); DBRU collection records from dung of elephant (1), rhinoceros (1), zebra (1).
Temporal activity: Diurnal flight activity primarily during the summer rainy season (Oct. to Mar.).
Bioregions South Africa: Lowveld (SVl) (Savanna Biome); marginal in two other bioregions.
Assessment rationale: EOO = 273 965 km^2 (gross estimate); AOO would presumably be smaller because of bias to dung of monogastric herbivores; this association is reflected by the disjunct patchy distribution primarily in game reserves into which the ranges of large indigenous herbivores have contracted; as quantitative ecological data is limited; the species is assessed as Data Deficient (DD) although it would probably qualify for Least Concern (LC) owing to widespread occurrence in various reserves.
Conservation measures: Quantitative data on habitat associations and a survey to determine full EOO and AOO are required before an adequate assessment may be made of conservation status; protected in various game reserves and national parks, including Hluhluwe–iMfolozi, Ithala, Kruger (South Africa), Masai Mara (Kenya).



Genus *Ixodina* Roth, 1851

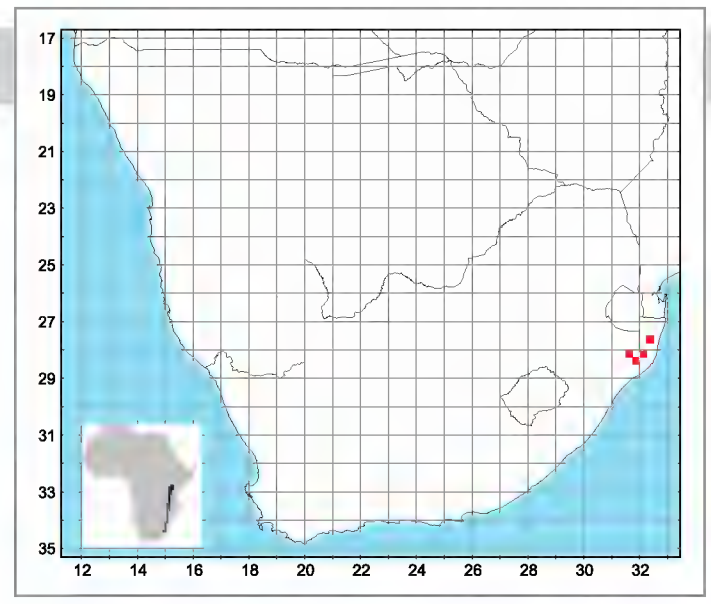
Type species and designation: *Ixodina abyssinica* Roth, 1851, by monotypy.
Synonyms: None.
Last review: Entire genus reviewed by Krikken (2009).

Ixodina Roth, 1851, was revalidated from synonymy with *Drepanocerus* Kirby, 1828, by Krikken (2009). It now comprises five species in moist savannas of the Afrotropical region following the recent transfer of three species to the new genus, *Paraixodina* Roggero, Barbero & Palestrini, 2015. Roggero et al. (2015) note that there are no significant differences between the genitalia and epipharynx of four *Ixodina* species described by Endrödi (1971, 1976). The alpha taxonomy may require revision.

A single species is found in NE savannas of KwaZulu-Natal, South Africa, where it has been recorded only from game reserves. However, it ranges into the tropics as S to E, and, E to W African subspecies.

Ixodina abyssinica

Roth, 1851



subsp. *abyssinica* Roth, 1851
subsp. *tangana* (Endrödi, 1971)

Global: DD

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *I. abyssinica*: 'Tigré in N. Abyssinien' [Tigray, N Ethiopia]; as *Drepanocerus abyssinicus* Roth subsp. *tanganus*: 'Mt. Meru E slope, 5700 feet' [N Tanzania].

Taxonomy: Accepted species in the subfamily Drepanocerina; southern African material should be compared with types of subspecies; sexual dimorphism (head, prothoracic disc) characters varying in prominence with body size.

Distribution: Widespread in dry to moister savanna regions of Africa; subsp. *abyssinica*: W to NE Africa, Guinea (Bissau), Guinea (Conakry), Ivory Coast, Niger, Cameroon, Democratic Republic of the Congo (DRC), Ethiopia, Djibouti; subsp. *tangana*: E to S Africa, Kenya, Tanzania, Mozambique, South Africa (see range map).

Locality data (mean ± SD, range): Altitude: 229 ± 145, 55–450 m; annual rainfall: 888 ± 110, 743–1 075 mm; annual temperature (max. + min. /2): 21.3 ± 0.9, 20.5–22.8°C (N=6).

Habitat: No quantitative assessment; limited DBRU collection records from sand (2) in open woodland (1) and pasture (1).

Food types: No quantitative assessment; limited DBRU collection records from dung of cattle (2), buffalo (1), rhinoceros (1).

Temporal activity: Diurnal flight activity, primarily in the summer rainy season (Aug. to Apr.).

Bioregions South Africa: S extremity of Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 347 255 km^2 (underestimated); AOO would be smaller and limited to moister climate; restricted distribution pattern possibly a mix of localisation and collection artefact due to small body size; ecologically poorly known; apparently widespread, so may deserve Least Concern (LC) status, however, currently assessed as Data Deficient (DD).

Conservation measures: Assessment of conservation status would be improved by more comprehensive data as known range may be underestimated and ecological associations are poorly known; in South Africa, all known localities protected in uMkhuze and Hluhluwe–iMfolozi game reserves.

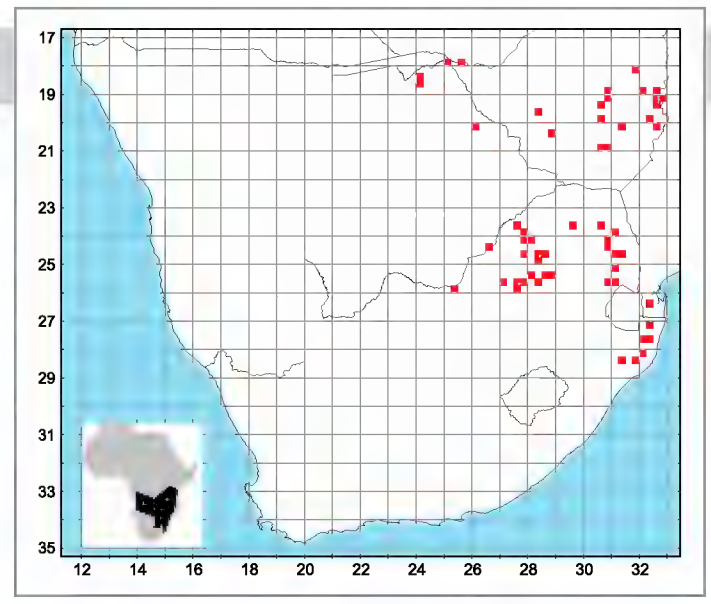
Genus *Latodrepanus* Krikken, 2009

Type species and designation: *Drepanocerus laticollis* Fahraeus, 1857, by original designation.
Synonyms: = *Drepanellus* Barbero, Palestrini & Roggero, 2009b: Type species: *Drepanocerus laticollis* Fahraeus, 1857, by original designation.
Last review: Entire genus reviewed by Krikken (2009), new species added by Barbero et al. (2009b).

The Afrotropical genus, *Latodrepanus* Krikken, 2009, now comprises three species following the description of two new species from West (Guinea) and SE Africa (Malawi) (Barbero et al. 2009b) and the transfer of three W to E or E African species to the new genus *Epidrepanus* Roggero, Barbero & Palestrini, 2015. A single species occurs in South Africa. It shows a dry, sandy, savanna distribution from S to S Central to E Africa.

Latodrepanus laticollis

(Fahraeus, 1857)



No synonyms

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Drepanocerus laticollis*: 'juxta fluvium Limpopo' [near Limpopo River, southern Africa].

Taxonomy: Accepted species in the subfamily, Drepanocerina.

Distribution: Moist savanna on sandy soils from S to E Africa: NE South Africa, NE Botswana, Angola, Zimbabwe, Zambia, Mozambique, Democratic Republic of the Congo (DRC), Tanzania, Kenya; citations from W Africa (Senegal, Guinea, Benin) represent confusion with other *Latodrepanus* or *Epidrepanus* species; disjunctions may partly reflect distribution of suitable climate and sandy soils.

Locality data (mean ± SD, range): Altitude: 832 ± 427, 0–1 462 m; annual rainfall: 701 ± 184, 418–1 275 mm; annual temperature (max. + min. /2): 20.4 ± 1.7, 17.3–24.7°C (N=80).

Habitat: In Gauteng bushveld: extreme bias to deep sand (2 080) compared to sandy clay loam (54) with bias to open woodland (1 714) compared to grassland (386) or shaded thickets (34); DBRU collection records biased to sandy soils: sand (20), sandy loam (12), sandy clay loam (8) in woody vegetation: grassland/pasture (12), shrubland (8), open woodland (19), shaded thicket (1).

Food types: At Phalaborwa: extreme bias to herbivore dung (ruminant cattle: 240; monogastric elephant: 169) compared to omnivore dung (pig: 9); similar in Gauteng bushveld: cattle (327), horse (206), pig (14), carrion (0); DBRU collection records from dung of cattle (42), rhinoceros (2), donkey (1), waterbuck (1), human (1).

Temporal activity: Diurnal flight activity peaking at midday and early afternoon (12:00–16:00) in Gauteng bushveld; primarily active in the summer rainy season (Oct. to Apr.); abundant from Oct. to Jan., tailing off Feb. to Apr., rare May to July; at Phalaborwa: more abundant in warm sunny weather soon after heavy rainfall (951) than on a hot dry day (157) or a warm cloudy day following light rainfall (30).

Ecoregions Botswana, Zimbabwe, Mozambique: Southern African Bushveld (AT0717), Southern Miombo Woodlands (AT0719), moister W of Zambezian and Mopane Woodlands (AT0725); Maputaland Coastal Forest Mosaic (AT0119).

Bioregions South Africa: Primarily centred on Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 4 469 700 km^2 (rough estimate); AOO would be smaller according to soil and vegetation specialisation; clearance of woody vegetation on sandy soils would presumably reduce population density; however, very widespread and protected in various reserves; therefore, assessed as Least Concern (LC).

Conservation measures: None recommended; protected in Kruger National Park, Leeuwfontein and Tswaing nature reserves (South Africa).

Genus *Liatongus* Reitter, 1893

Type species and designation: *Onthophagus phanaeoides* Westwood, 1839, by subsequent designation (Arrow 1931).
Synonyms: None (but see below).
Last review: Entire genus reviewed by Janssens (1953); new species added by Balthasar (1956, 1964a), Scheuern (1988), Král and Rejsek (1999); two species removed to other genera *Attavicinus monstosus* (Bates 1887), *Paroniticellus festivus* (Steven 1809); one species transferred from *Oniticellus* Dejean, 1821, may be misclassified within *Liatongus* (often cited as *Scaptodera rhadamistus* (Fabricius, 1775)).

Because of common usage, *Liatongus* Reitter, 1893, is retained here as the generic name, although it has recently been noted (Branco 2011) that it is a junior synonym of *Onthosphaenus* Motschulsky, 1860 (Type species: *Scarabaeus vertagus* Fabricius, 1798, by subsequent designation (Paulian 1986)).

Liatongus is widespread in moist forest, savanna and upland grassland regions where it is represented by a total of 44 species in the Afrotropical (16), Oriental (23), Palaearctic (3) and Nearctic regions (2), with a further three species shared between the Oriental and Palaearctic. One further Oriental species, formally transferred by Lumaret and Moretto (1983) from *Oniticellus* Dejean, 1821, into the *Liatongus* subgenus *Paraliatongus* Balthasar, 1963d, may be misclassified and is often cited within the genus *Scaptodera* Hope, 1837 (see above).

Since Janssens' review (1953), the single Neotropical species has been removed from *Liatongus* into the new genus *Attavicinus* Philips & Bell, 2008. A Palaearctic species has been removed into the genus, *Paroniticellus* Balthasar, 1963d (see above). However, as presently constituted the genus remains paraphyletic (Philips 2016) based on relationships of two species, one Afrotropical, one Nearctic.

Only two *Liatongus* species are found within the study area of Namibia, Botswana and South Africa. One of these is apparently an undescribed forest endemic with a restricted range (no species account prepared). The other is widespread in moist E savannas and grasslands with a range extending into the S central and E tropics.

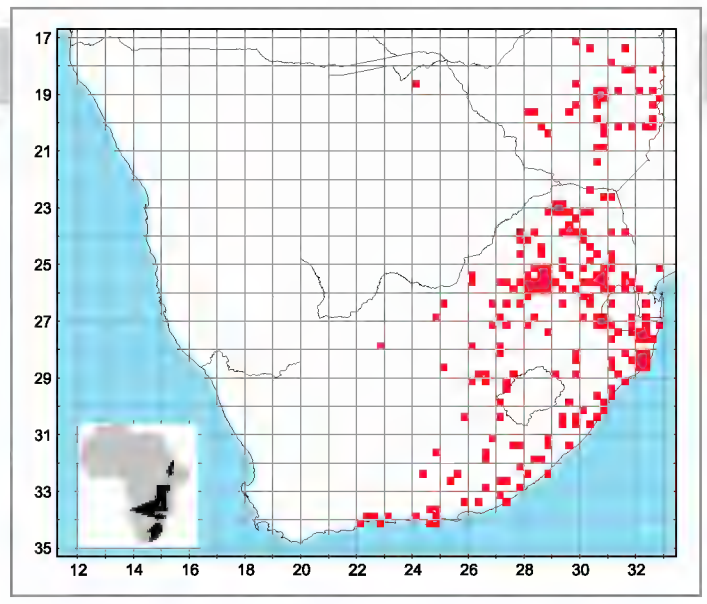
Liatongus militaris

(Castelnau, 1840)

= *Oniticellus tridens* Roth, 1851
= *Oniticellus quadrituberculatus* van Lansberge, 1886

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: As *Oniticellus militaris*: 'Cap de Bonne-Espérance' [Cape of Good Hope, South Africa]; *O. tridens*: 'Tigré, N. Abyssinien' [Tigray Region, Ethiopia]; *O. quadrituberculatus*: 'l'Afrique Occidentale' [Humpata, Angola].

Taxonomy: Accepted species; limited sexual dimorphism (head, prothoracic disc).

Distribution: Moist grassland and savanna from S and S Central to NE Africa: South Africa, Zimbabwe, Mozambique, Angola, Kenya, Tanzania; marginal in N Botswana; also cited from Eritrea, Sudan, Egypt.

Locality data (mean ± SD, range): Altitude: 949 ± 532, 0–2 274 m; annual rainfall: 720 ± 181, 309–1 659 mm; annual temperature (max. + min. /2): 18.4 ± 2.4, 10.6–25.2°C (N=315).

Habitat: In Gauteng bushveld: strong bias to finer-grained soils: deep sand (66), sandy clay loam (1 261) in open vegetation: grassland (1 013), open woodland (297), shaded thickets (17); partly supported by DBRU collection records: sand (35), sandy loam (44), sandy clay loam (49), clay (14) in grassland/pasture (97), scrub/shrubland (10), open woodland (19), thickets (3).

Food types: At Phalaborwa: strong bias to dung of elephant (22) rather than that of cattle (4) or pig (0); DBRU collection records dominated by common herbivore dung types outside of reserves: cattle (163), buffalo (6), elephant (1), horse (1).

Temporal activity: Diurnal flight activity primarily during the summer rainy season (Oct. to Apr.); at Phalaborwa: frequency much greater in hot, dry conditions (20) compared to warm cloudy conditions following light rainfall (4) or warm sunny weather soon after heavy rainfall (2).

Ecoregions Botswana, Zimbabwe: Primarily Southern Miombo Woodlands (AT0719), Southern African Bushveld (AT0717).

Bioregions South Africa: Centred in Savanna (SV), Grassland (G), Indian Ocean Coastal Belt (CB) biomes; Bioregions: Central Bushveld (SVcb), Lowveld (SVl), Mesic Highveld Grassland (Gm), Dry Highveld Grassland (Gh), Sub-Escarpment Grassland (Gs); also Albany Thicket Biome (AT), SE Fynbos Biome, primarily in transformed habitats; marginal in Eastern Kalahari Bushveld (SVk).

Assessment rationale: EOO = 3 632 435 km² (underestimated); widespread with a bias to open habitats and a high frequency of records from cattle dung in farmland despite a measured bias to elephant dung; assessed as Least Concern (LC).

Conservation measures: None recommended; protected in Hluhluwe–iMfolozi Game Reserve (South Africa) and Gorongosa National Park (Mozambique).

Genus *Oniticellus* Dejean, 1821

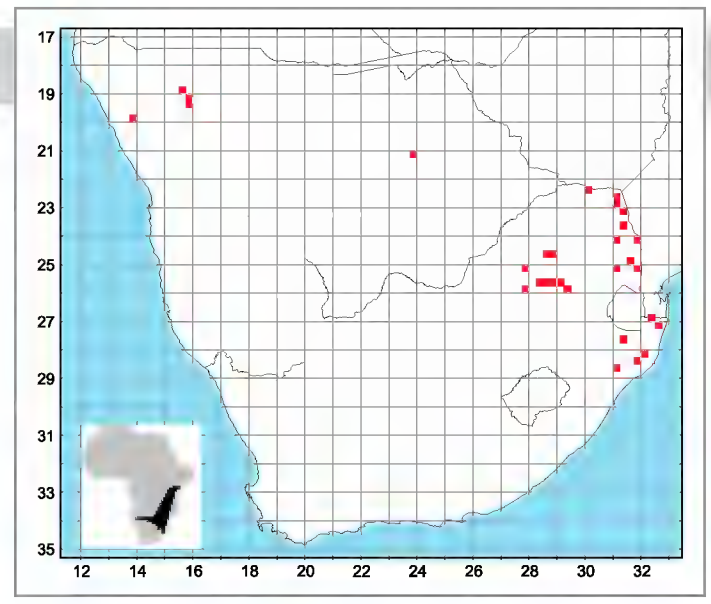
Type species and designation: *Scarabaeus cinctus* Fabricius, 1775, by subsequent designation (Arrow 1931).
Synonyms: = *Pseudoniticellus* Kraatz, 1895: Type species: *Oniticellus planatus* Castelnau, 1840, by monotypy.
Last review: Entire genus reviewed by Janssens (1953) with one species, thereafter, formally transferred to *Paraliatongus* Balthasar, 1963d (Lumaret & Moretto 1983); new species added by Balthasar (1964a), Biswas and Chatterjee (1985).

Addition and subtraction of species following the review of Janssens (1953), reduces membership of *Oniticellus* Dejean, 1821, to seven, perhaps eight, species found in the Afrotropical (5) or Oriental regions (2 +?1). The included species all show essentially endocoprid breeding habits and have a history of misidentification and assignment to different genera, including *Pseudoniticellus* Kraatz, 1895; *Liatongus* Reitter, 1893; and *Pseudoniticellus sensu* Paulian, 1945. Two new species added after Janssens review comprise an Afrotropical forest species (*O. pseudoplanatus* Balthasar, 1964a) and an Oriental species (*O. gayeni* Biswas & Chatterjee, 1985) that requires validation as it is cited from the same droppings as a close relative. One Oriental species subtracted after Janssens review has been variously cited as a species of *Paraliatongus* Balthasar, 1963; *Liatongus* (*Paraliatongus*), *Liatongus* or *Scaptodera* Hope, 1837 (cf. *S. rhadamistus* (Fabricius, 1775)).

In South Africa, Botswana and Namibia, *Oniticellus* is represented by four widespread species, all assessed as Least Concern (LC), two with ranges extending into the E tropics and two with ranges extending into the E tropics and onwards into W Africa. In southern Africa, the species are centred on elephant or equine dung in savanna (1); or various dung types in E savanna (1); E savanna plus E upland grassland and the S Cape coast (1); or just E upland grassland and the S Cape coast (1). These four species either construct brood chambers in droppings without tunnelling in the soil (2) or they construct brood chambers in the soil in contact with the dropping (2). Monitoring of two species for an entire year has shown that they remain active as adults throughout the rainy and dry seasons without any detected dormancy.

Oniticellus egregius

Klug, 1855

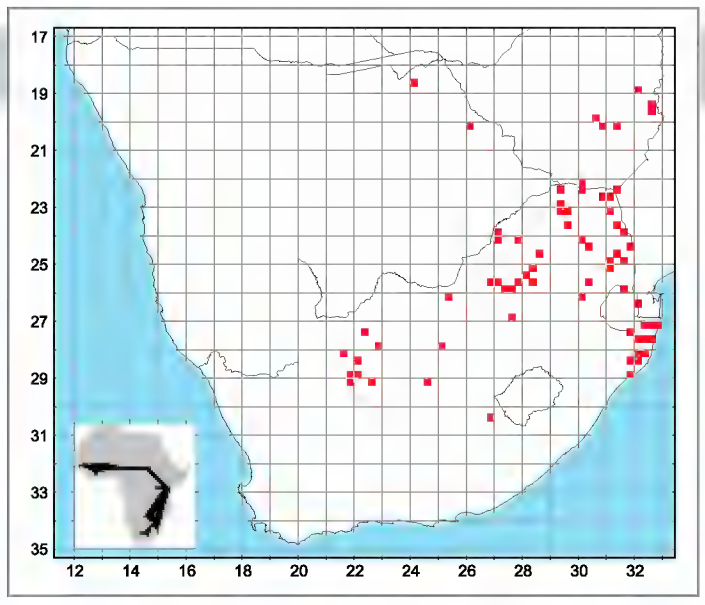


No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Tette' [Tete, Central Mozambique].
Taxonomy: Accepted species, once separated into the genus *Pseudoniticellus sensu* Paulian, 1945, but last reviewed as *Oniticellus* (Janssens 1953).
Distribution: Widespread in dry savanna from S to E Africa: South Africa, Namibia, Botswana, Mozambique, Tanzania, Kenya; also reported from Zimbabwe, Democratic Republic of the Congo (DRC), Somalia.
Locality data (mean ± SD, range): Altitude: 748 ± 450, 33–1 524 m; annual rainfall: 597 ± 156, 263–904 mm; annual temperature (max. + min. /2): 20.7 ± 2.3, 15.6–23.6°C (N=38, exact records).
Habitat: No quantitative assessment; limited DBRU collection records from sandy loam (3) in grassland/pasture (1) or open woodland (3).
Food types: No adequate quantitative assessment; at Phalaborwa (2) and in Botswana (4): only sampled to elephant dung; DBRU collection records from dung of elephant (6), rhinoceros (1) and horse (1).
Temporal activity: Diurnal flight activity recorded in the summer rainy season (Oct. to Mar.); may show greater seasonality than strictly endocoprid *Oniticellus* species as nests are sited in pits in the soil under the edge of droppings and contain clay coated broods that are not tended by the parent female during larval development.
Ecoregions Namibia, Botswana: Namibian Savanna Woodlands (AT1316), Angolan Mopane Woodlands (AT0702), Kalahari Acacia-Baikiaea Woodlands (AT0709).
Bioregions South Africa: Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome); margins of two other bioregions.
Assessment rationale: EOO = 2 407 180 km^2; AOO much smaller owing to specialisation to coarse-fibred dung of monogastric herbivores whose distribution has largely contracted to within the borders of game reserves or to areas such as Gauteng (South Africa) where there are adequate populations of indigenous (zebra) or domestic equines (horse); however, assessed as Least Concern (LC) owing to widespread protection in many game reserves which account for 65% of available southern African records (46).
Conservation measures: Conservation status of this species would be dependent on continuing protection of large monogastric herbivores in savanna reserves and maintenance of equine populations elsewhere; assessment of conservation status would be improved by quantitative data on habitat associations and how these might further influence the AOO; protected in various national parks and game reserves including Kruger, uMkhuze, Hluhluwe–iMfolozi (South Africa), Etosha (Namibia), Manyara (Tanzania), Tsavo, Masai Mara, Amboseli, Meru (Kenya).



Oniticellus formosus

Chevrolat, 1830

= *Oniticellus pictus* Hausmann *sensu* Péringuey, 1901 (*pars*)
= *Oniticellus parapictus* Balthasar, 1941a

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. formosus*: 'Sénégal' [Senegal]; *O. pictus sensu* Péringuey (*pars*): 'Transvaal (Rustenburg)' [South Africa]; *O. parapictus*: 'Senegal'.
Taxonomy: Accepted species assigned to the genus, *Liatongus* Reitter, 1893, by d'Orbigny (1916), but reviewed as *Oniticellus* by Janssens (1953).
Distribution: Mainly in dry savanna from W to E to southern Africa: Senegal, Côte d'Ivoire, Niger, Nigeria, Kenya, Tanzania, Mozambique, Zimbabwe, Botswana, South Africa; also reported from Mauritania, Angola.
Locality data (mean ± SD, range): Altitude: 752 ± 471, 8–1 706 m; annual rainfall: 608 ± 207, 205–1 168 mm; annual temperature (max. + min. /2): 20.4 ± 2.2, 14.4–25.2°C (N=77).
Habitat: In Gauteng bushveld: bias to finer-grained soils: sandy clay loam (96) rather than deep sand (19) where there is greater dung removal, also bias to more open habitats: grassland (80), open woodland (34) rather than shaded thickets (1); largely supported by DBRU collection records: sand (13), sandy loam (12), sandy clay loam (9), clay (7), in grassland/pasture (22), shrub/woodland (17).
Food types: At Phalaborwa: strong bias to elephant dung (32) as opposed to that of cattle (2) and pig (0); similar results in Botswana: elephant (16), cattle (2), sheep (3), pig (1); at Abokouamekro (Côte d'Ivoire): recorded to cattle (41), but not pig dung; DBRU collection records primarily from ruminant herbivore dung: cattle (33), buffalo (6), rather than monogastric herbivore dung: elephant (4), rhinoceros (1), donkey (1); also waterbuck (1).
Temporal activity: Diurnal flight activity; recorded during every month of the year; probably because this species does not tunnel in the soil and therefore does not remain dormant in tunnels during unsuitably cold weather; at Phalaborwa: frequency much greater in hot, dry conditions (29) than in warm cloudy conditions following light rainfall (0), or in warm sunny conditions soon after heavy rainfall (6); in Gauteng bushveld: greatest breeding success within cattle pads at the end of the dry season (Aug., Sept.) when dung removal is minimal and temperatures are increasing.
Ecoregions Botswana, Zimbabwe: Zambezian and Mopane Woodlands (AT0725), E Kalahari Acacia-Baikiaea Woodlands (AT0709), Southern Miombo Woodlands (AT0719).
Bioregions South Africa: Centred in Central Bushveld (SVcb), Lowveld (SVl), Mopane (SVmp) (Savanna Biome); also N Indian Ocean Coastal Belt Biome (CB) with sporadic occurrence in Eastern Kalahari Bushveld (SVk), NE Bushmanland (NKb).
Assessment rationale: EOO = 4 827 535 km^2; strong bias to large droppings of herbivores reflects endocoprid breeding habits (nest constructed within dropping containing broods that are tended by parent female during larval development); population density is low reflecting exploitation competition with dung-burying beetles and, probably, density dependence of breeding sites within dung (primarily, one nest per cattle pad); over most of the range elephant droppings no longer occur; however, extremely widespread, therefore, assessed as Least Concern (LC).
Conservation measures: None recommended; commonly recorded in low numbers from cattle dung in farmland despite a measured bias to elephant dung; protected in Kruger National Park and Hluhluwe–iMfolozi Game Reserve.

Oniticellus pictus

(Hausmann, 1807)

= *Oniticellus pictus* Péringuey, 1901 (*pars*)
= *Oniticellus pictus orientalis* Janssens, 1953

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Aphodius pictus*: Not stated; *O. pictus* Péringuey: 'Cape Colony (Uitenhage, Graham's Town, Queen's Town, Griqualand West, Knysna, Somerset East), Natal (Frere, Durban, Maritzburg)' [Eastern Cape, South Africa; KwaZulu-Natal citations may be either *O. pictus* or *O. formosus* Chevrolat]; subsp. *orientalis*: 'Est du Congo Belge: Parc National Albert' [Virunga National Park, E Democratic Republic of the Congo (DRC)].

Taxonomy: Accepted species.

Distribution: Disjunct distribution on the East Central African highlands (Democratic Republic of the Congo (DRC)) and the South African Highveld to SE coastal lowlands: additional reports from Rwanda, Tanzania; Mozambique report requires validation; Guinea presumably an error.

Locality data (mean ± SD, range): Altitude: 834 ± 701, 16–2 194 m; annual rainfall: 661 ± 188, 412–1 065 mm; annual temperature (max. + min. /2): 16.5 ± 2.0, 11.0–20.3°C (N=35).

Habitat: No quantitative assessment; DBRU collection records only from finer-grained soils: sandy loam (6), sandy clay loam (10), clay (1), primarily in grassland/pasture (12), less frequently in shrub/woodland (4).

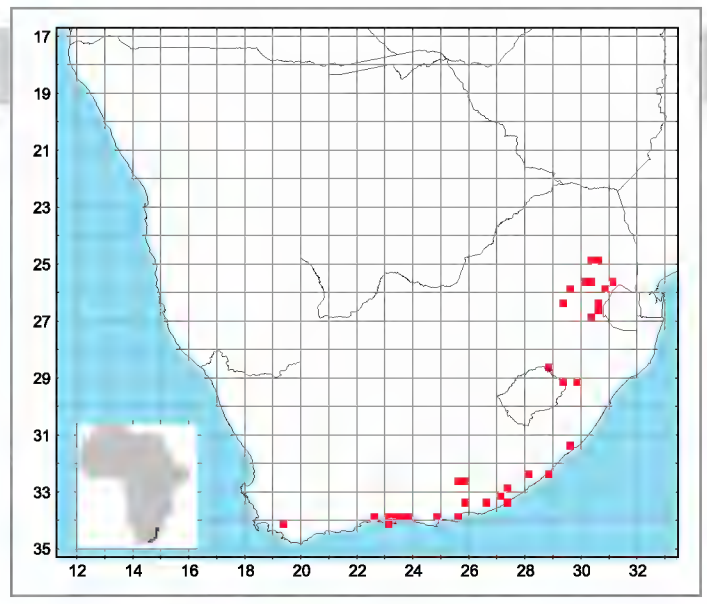
Food types: No quantitative assessment; DBRU collection records mainly from cattle dung (23), rarely horse dung (1).

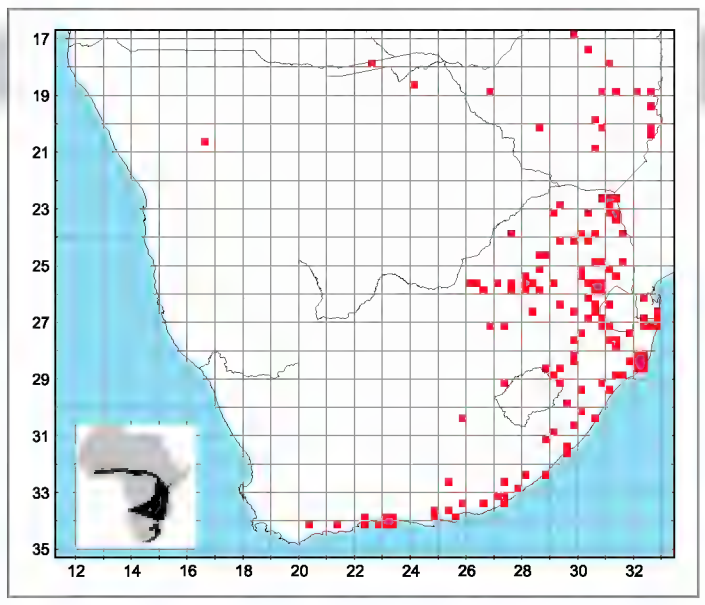
Temporal activity: Diurnal flight activity; recorded during both the dry (May, Aug., Sept.) and rainy seasons (Oct. to Mar.); several individuals observed clustered together in the centre of a cattle pad during a snow storm over natural grassland (Machadodorp [= Makhado] 16 km E), reflecting non-soil tunnelling, endocoprid habits (breed within droppings).

Bioregions South Africa: E Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs) (Grassland Biome); S Indian Ocean Coastal Belt Biome (CB); Albany Thicket Biome (AT); transformed S coastal habitats in Fynbos Biome.

Assessment rationale: EOO = 131 510 km^2; widely recorded in low population density from cattle dung in farmland; owing to widespread distribution, not thought to be threatened, thus, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, particularly whether or not pasture improvement influences its occurrence; not known from any nature reserve at the present time.





Oniticellus planatus

Castelnau, 1840

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Cap de Bonne-Espérance' [Cape of Good Hope, South Africa].

Taxonomy: Accepted species assigned to the genus *Pseudoniticellus* Kraatz, 1895, then to *Liatongus* Reitter, 1893, by d'Orbigny (1916), but reviewed as *Oniticellus* by Janssens (1953).

Distribution: Mainly in warmer moist savanna and warmer moist grasslands from W to E to southern Africa: Côte d' Ivoire, Kenya, Tanzania, Mozambique, Angola, Zimbabwe, NE Namibia, N Botswana, Eswatini, South Africa; also reported from Guinea (Conakry), Central African Republic, Democratic Republic of the Congo (DRC), Ethiopia, Somalia, Burundi, Rwanda.

Locality data (mean ± SD, range): Altitude: 790 ± 583, 0–2 194 m; annual rainfall: 731 ± 195, 365–1 659 mm; annual temperature (max. + min. /2): 18.8 ± 2.7, 11.0–25.2°C (N=186).

Habitat: No adequate quantitative data; DBRU collection records from sand (14), sandy loam (24), sandy clay loam (23), clay (8) in grassland/pasture (45), shrub/woodland (21), forest (2).

Food types: No adequate quantitative data; both at Phalaborwa and in Botswana: recorded only to elephant dung (5 at each), not ruminant herbivore or omnivore dung; however, DBRU collection records primarily from ruminant herbivore dung: cattle (80), buffalo (4); also monogastric herbivore dung: elephant (13), rhinoceros (4), horse (2), zebra (1).

Temporal activity: Diurnal flight activity; recorded during every month of the year; probably because this species is not known to tunnel in the soil under field conditions or to remain dormant in tunnels during unsuitably cold weather; in Gauteng bushveld: greatest breeding success at the interface between soil and cattle pads was at the end of the cool, dry season (Aug., Sept.) when dung burial is minimal and temperatures are increasing.

Ecoregions Namibia, Botswana, Zimbabwe, Mozambique: Southern Miombo Woodlands (AT0719), Southern African Bushveld (AT0717), moister margins of Zambezian and Mopane Woodlands (AT0725), Maputaland Coastal Forest Mosaic (AT0119).

Bioregions South Africa: Central Bushveld (SVcb), Lowveld (SVl), Mopane (SVmp) (Savanna Biome); sporadic occurrence in Grassland Biome with greater frequency only in warmer E Mesic Highveld Grassland (Gm) and N Sub-Escarpment Grassland (Gs); Indian Ocean Coastal Belt (CB) and Albany Thicket (AT) biomes; transformed habitats in Eastern Cape part of Fynbos Biome.

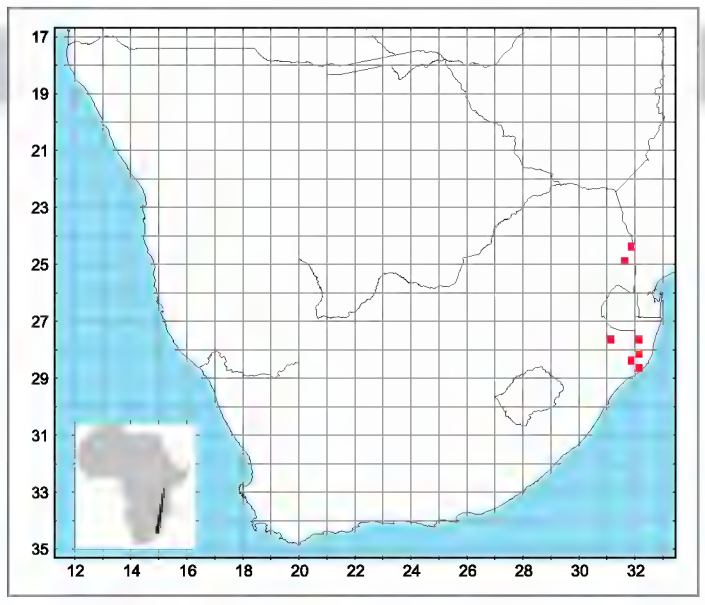
Assessment rationale: EOO = 4 837 160 km^2; bias to large droppings of herbivores reflects endocoprid breeding habits (nest constructed at dropping/soil interface containing broods that are tended by female parent during larval development); population density is low, reflecting exploitation competition with dung-burying beetles and probable density dependence of breeding sites within dung (primarily, one nest per cattle pad); over most of the range elephant droppings no longer occur; however, extremely widespread, therefore, assessed as Least Concern (LC).

Conservation measures: None recommended; commonly recorded in low numbers from cattle dung in farmland despite a measured bias to elephant dung; protected in moister parts of Kruger National Park and Hluhluwe–iMfolozi Game Reserve.

Genus *Paraixodina* Roggero, Barbero & Palestrini, 2015

Type species and designation: *Drepanocerus runicus* Arrow, 1909, by original designation.
Synonyms: None.
Last review: Genus created and reviewed with a morphological phylogeny by Roggero et al. 2015.

Paraixodina Roggero, Barbero & Palestrini, 2015, currently comprises three very small-bodied species from savannas in the E Afrotropical (2) and E Oriental regions (1). The two Afrotropical species range from E Savanna of South Africa into the E tropics. Both are primarily associated with monogastric herbivore dung.



Paraixodina freyi

(Janssens, 1953)

No synonyms

Global: DD (see IUCN Red List as *Ixodina freyi* – DD)

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Drepanocerus freyi*: 'Zululand : Hluhluewe' [presumably, Hluhluwe Game Reserve, KwaZulu-Natal, South Africa].

Taxonomy: Accepted species in the subfamily, Drepanocerina.

Distribution: Limited patchy records along the E seaboard of Africa; moist lowland savanna in NE South Africa, upland grassland in Kenya (1 500 m); also cited from Tanzania.

Locality data (mean ± SD, range): Altitude: 246 ± 253, 62–879 m; annual rainfall: 795 ± 135, 566–982 mm; annual temperature (max. + min. /2): 21.2 ± 1.2, 18.4–22.4°C (N=9).

Habitat: No quantitative assessment; extremely limited DBRU collection records from sandy clay loam (1), clay (1) in open woodland (2).

Food types: No quantitative assessment; extremely limited DBRU collection records from dung of cattle (1), rhinoceros (1); recorded from zebra dung in Kenya (1).

Temporal activity: Diurnal flight activity primarily in the summer rainy season (Nov. to Feb., May).

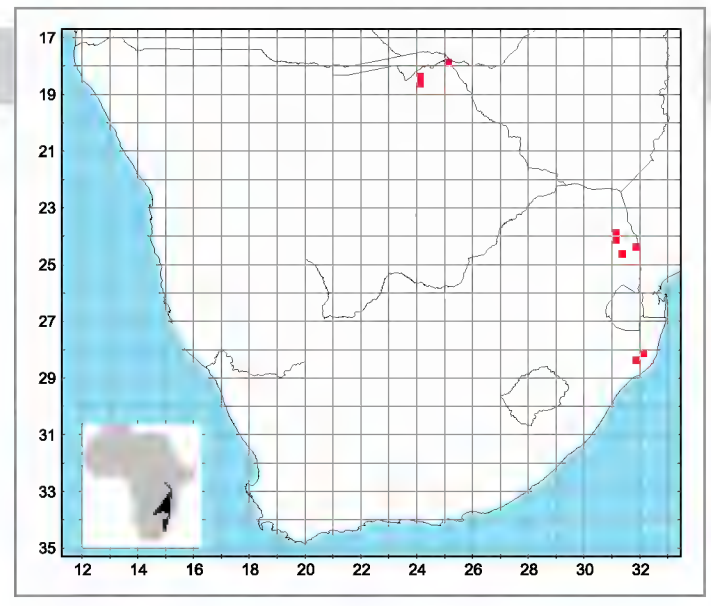
Bioregions South Africa: Centred on Lowveld (SVl) (Savanna Biome), marginal in extreme N tip of Sub-Escarpment Grassland (Gs) (Grassland Biome).

Assessment rationale: EOO = 450 215 km^2 (gross estimate); poorly known ecologically; unclear if soil type or vegetation type influences occurrence; food associations unclear although all but one of the available records are from game reserves where elephants and rhinoceros occur; thus, known range in South Africa mostly protected; assessed as Data Deficient (DD).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, particularly dung type associations; *P. freyi* is thought to be a monogastric dung specialist, which would have important conservation implications as regards a possibly highly restricted AOO within a large EOO; protected in Hluhluwe–iMfolozi and uMkhuze game reserves plus Kruger National Park (South Africa), Masai Mara Game Reserve (Kenya).

Paraixodina saegeri

(Balthasar, 1963e)



No synonyms

Global: DD

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Drepanocerus saegeri*: 'National Parc de la Garamba' [Garamba National Park, NE Democratic Republic of the Congo (DRC)].

Taxonomy: Accepted species in the subfamily, Drepanocerina; morphology of southern African and Tanzanian individuals matches original description, but identity should be validated by comparison with type material.

Distribution: Limited patchy records in moist lowland savanna along the E seaboard of Africa; South Africa, Botswana, Tanzania, NE Democratic Republic of the Congo (DRC); also cited from Kenya; citation from Côte d'Ivoire requires validation; disjunctions on map reflect samples recorded within or close to game reserves where monogastric herbivores occur.

Locality data (mean ± SD, range): Altitude: 480 ± 311, 117–1 000 m; annual rainfall: 668 ± 142, 529–904 mm; annual temperature (max. + min. /2): 21.7 ± 0.6, 20.5–22.5°C (N=12).

Habitat: No quantitative assessment; observed on sand, sandy loam and sandy clay loam in open woodland and forest.

Food types: At Phalaborwa: extreme bias to monogastric herbivore dung (elephant: 27) compared to dung of ruminant herbivores (cattle: 1) and omnivores (pig: 2); one DBRU collection record from rhinoceros dung; also recorded in zebra dung.

Temporal activity: Diurnal flight activity in the summer rainy season (Nov. to Feb.); at Phalaborwa: primarily active on a hot sunny day (28), few active in warm cloudy weather following light rain (2) or in warm weather soon after heavy rainfall (0).

Ecoregions Botswana: Zambezian and Mopane Woodlands (AT0725).

Bioregions South Africa: Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 1 073 235 km^2 (gross estimate for E seaboard); AOO would be much smaller because of range contraction by large indigenous monogastric herbivores to whose dung *P. saegeri* is specialised; limited patchy records probably a collection artefact related to both dung type specialisation and small body size; probably not threatened due to large range and protection in various reserves; however, poorly known and assessed as Data Deficient (DD).

Conservation measures: Assessment of conservation status would be improved by quantitative data on habitat associations and further survey data to determine full EOO and AOO; protected in various national parks and game reserves, including Hluhluwe–iMfolozi and Kruger (South Africa), Chobe (Botswana), Manyara (Tanzania).

Genus *Tibiodrepanus* Krikken, 2009

Type species and designation: *Copris setosus* Wiedemann, 1823, by original designation.
Synonyms: = *Sulcodrepanus* Krikken, 2009: Type species: *Drepanocerus sulcicollis* Castelnau, 1840, by original designation.
Last review: All but one species of the genus reviewed by Barbero et al. (2011); phylogeny (Roggero et al. 2015).

Tibiodrepanus Krikken, 2009, currently comprises seven species found in moist forest, savanna or grassland of the Afrotropical (2), Oriental (4) or S Palaearctic (Afghanistan: 1) regions. The single species represented in moist SE grasslands of South Africa is widely represented across a range extending into the E and W tropics.

Tibiodrepanus sulcicollis

(Castelnau, 1840)

= *Drepanocerus dispar* Boheman, 1857

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Oniticellus sulcicollis*: 'Cap de Bonne-Espérance'; *D. dispar*: 'Caffraria meridionali.....Cap. Bonae Spei.' [both Cape of Good Hope, South Africa].

Taxonomy: Accepted species in the subfamily, Drepanocerina; sexual dimorphism varying in prominence with body size (prothoracic disc).

Distribution: Moist grassland from S to E to W Africa: South Africa, Mozambique, Democratic Republic of the Congo (DRC), Kenya, Ethiopia, Cameroon, Guinea (Conakry), Côte d'Ivoire; also cited from 13 other countries in S (1), E (4) and W (8) Africa.

Locality data (mean ± SD, range): Altitude: 893 ± 601, 55–2 140 m; annual rainfall: 725 ± 171, 389–1 065 mm; annual temperature (max. + min. /2): 16.6 ± 2.0, 11.3–22.6°C (N=38).

Habitat: No quantitative assessment; DBRU collection records all from finer-grained soils; sandy loam (7), sandy clay loam (5), clay (1) in open vegetation: grassland/pasture (11), scrub (2).

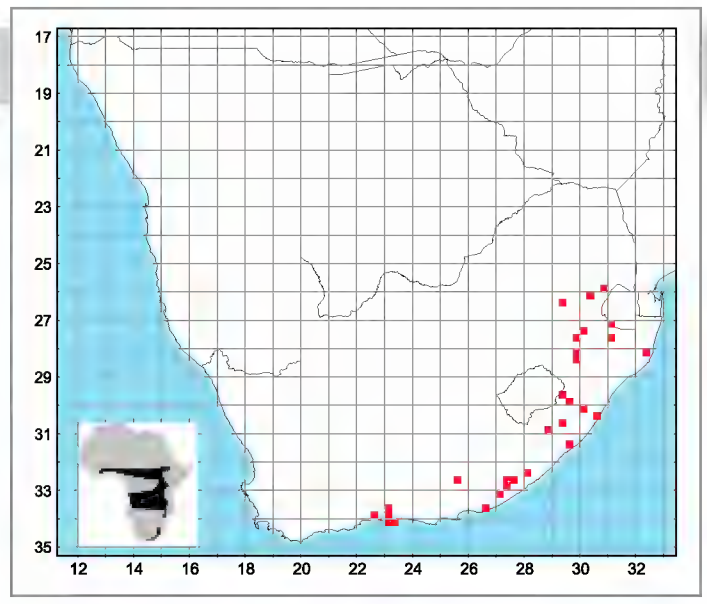
Food types: No adequate quantitative assessment; DBRU collection records entirely from cattle dung (14) although sampled to dung of horse (5) rather than cattle (1) in Ithala Game Reserve.

Temporal activity: Diurnal flight activity primarily in the summer rainy season (Oct. to Apr.).

Bioregions South Africa: E Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs) (Grassland Biome); Indian Ocean Coastal Belt Biome (CB); mostly transformed habitats in Albany Thicket (AT) and SE coastal Fynbos Biomes.

Assessment rationale: EOO = 5 683 200 km² based on limited data; in the SE: AOO centred on cool, moist climate; in the E: AOO centred on tropical uplands; in the W: AOO apparently centred on wet tropical lowlands; AOO smaller than EOO, but also, apparently, large with high frequency of records from cattle dung in open vegetation of farmland; therefore, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; protected in Ithala Game Reserve (South Africa).



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Genus *Tiniocellus* Péringuey, 1901

Type species and designation: *Oniticellus spinipes* Roth, 1851, by monotypy.
Synonyms: None.
Last review: Entire genus reviewed by Branco (2010).

After the review of Branco (2010), *Tiniocellus* Péringuey, 1901, currently comprises six species represented in the savannas of the Afrotropical (5) and W Oriental regions (1). In the study area of Namibia, Botswana and South Africa, the genus is represented by two species, both centred in E savanna with one showing a range extending into the S central and E tropics.

Tiniocellus eurypygus

Branco, 2010

subsp. *eurypygus* Branco, 2010
subsp. *transdrakensbergensis* Branco, 2010

Global: LC
Endemic: RSA, Eswatini

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: subsp. *eurypygus*: 'RSA, Limpopo, Potgietersrus' [Mokopane, Limpopo Province]; subsp. *transdrakensbergensis*: 'RSA, KwaZulu-Natal, Itala Reserve' [Ithala Game Reserve] [both South Africa].

Taxonomy: Accepted species.

Distribution: subsp. *eurypygus*: bushveld savanna, NW South Africa (red squares); subsp. *transdrakensbergensis*: NE lowland savanna, South Africa plus Eswatini (black squares).

Locality data (mean ± SD, range): subsp. *eurypygus*: altitude: 1 212 ± 146, 943–1 491 m; annual rainfall: 638 ± 45, 528–709 mm; annual temperature (max. + min. /2): 18.7 ± 0.8, 17.2–20.4°C (N=32). subsp. *transdrakensbergensis*: altitude: 467 ± 383, 55–1 736 m; annual rainfall: 700 ± 150, 436–964 mm; annual temperature (max. + min. /2): 21.1 ± 2.2, 14.0–23.7°C (N=35).

Habitat: In Gauteng bushveld, subsp. *eurypygus*: bias to deep sand (941) compared to sandy clay loam (282), strong bias to open woodland (1 043) compared to grassland (92) or shaded thickets (88) (cited as *T. spinipes* (Roth)); at Roodeplaat Nature Reserve: grassland (1.1), open woodland (6.3), shaded thickets (0.1); supported by DBRU collection records for both subsp. on sand (8), sandy loam (7), sandy clay loam (3) in pasture (2), open shrub/woodland (15).

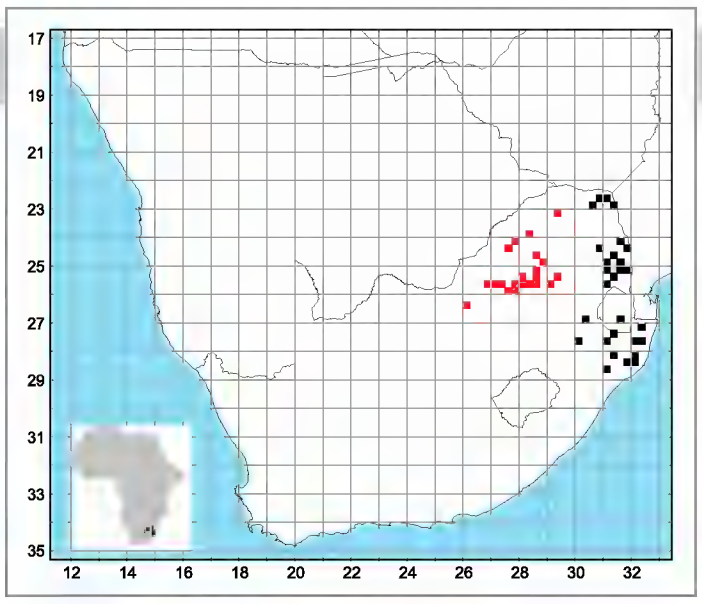
Food types: At Phalaborwa, subsp. *transdrakensbergensis*: bias to dung of monogastric herbivores (elephant: 117) compared to omnivores (pig: 55) or ruminant herbivores (cattle: 30); DBRU collection records for both subspp. from various dung types: elephant (2), rhinoceros (5), zebra (1), horse (3), baboon (1), cattle (8), buffalo (1), wildebeest (1), waterbuck (1).

Temporal activity: Diurnal flight activity recorded in most months (July to May); in Gauteng bushveld, subsp. *eurypygus*: primarily active in the rainy season from early to mid-summer (Oct. to Jan.), tailing off in late summer (Feb. to Apr.); very low activity in the cool dry season (May to Sept.); at Phalaborwa, subsp. *transdrakensbergensis*: less active on a warm, moist cloudy day (23) than on warm, moist sunny (96) or hot, dry sunny (84) days.

Bioregions South Africa: subsp. *eurypygus*: Central Bushveld (SVcb); subsp. *transdrakensbergensis*: Lowveld (SVl) (both Savanna Biome); marginal in three other bioregions.

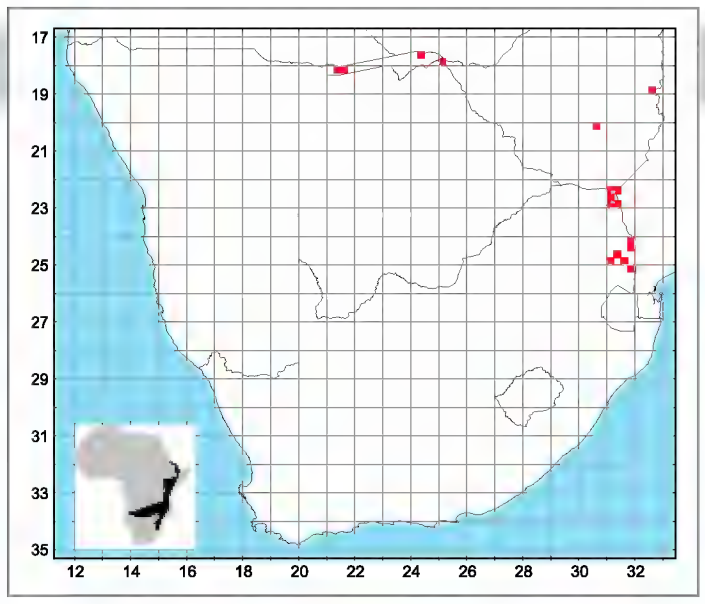
Assessment rationale: EOO = 123 625 km²; widespread in NE South African savanna, but population density would be influenced by clearance of partially shaded woody vegetation and contraction in ranges of monogastric herbivores (habitat transformation: 0–58% (SVl), 2–49% (SVcb)); however, frequently recorded in both reserves and farmland; therefore, assessed as Least Concern (LC).

Conservation measures: Continuing conservation of monogastric herbivores in woody vegetation would favour higher population density; protected in Kruger National Park (subsp. *transdrakensbergensis*) and various nature reserves: Leeuwfontein, Tswaing (subsp. *eurypygus*).



Subsp. *eurypygus*

Subsp. *transdrakensbergensis*



Tiniocellus spinipes

(Roth, 1851)

= *Oniticellus variegatus* Fahraeus, 1857
= *Onticellus humilis* Gerstaecker, 1871
= *Tiniocellus asmarensis* Balthasar, 1968

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Oniticellus spinipes*: 'Abyssinien' [Tigray, N Ethiopia]; *O. variegatus*: 'juxta fluvium Limpopo' [near Limpopo River, southern Africa]; *O. humilis*: 'Mbaramu' [Mbalamu, NE Tanzania]; *T. asmarensis*: 'Ost-Afrika: Aethiopien, Erythraea, Umgebung von Asmara' [environs of Asmara, Eritrea].

Taxonomy: Accepted species.

Distribution: Hot savanna from SE to NE Africa: NE South Africa, Mozambique, SE Zimbabwe, N Botswana, NE Namibia, S Angola, S Democratic Republic of the Congo (DRC), Zambia, Malawi, Tanzania, Kenya, Ethiopia, Eritrea, Somalia; one tentative record from the Sahel in Burkina Faso, W Africa.

Locality data (mean ± SD, range): Altitude: 470 ± 346, 28–1 397 m; annual rainfall: 636 ± 219, 383–1 177 mm; annual temperature (max. + min. /2): 22.6 ± 1.8, 17.1–25.5°C (N=27).

Habitat: No quantitative assessment; limited DBRU collection records from sandy loam (1), sandy clay loam (2), clay (1) in open woodland (4), forest (1).

Food types: No quantitative assessment; DBRU collection records from dung of elephant (8), baboon (1), buffalo (1).

Temporal activity: Diurnal flight activity, primarily during the summer rainy season (Sept. to Mar.).

Ecoregions Namibia, Botswana, Zimbabwe: Zambezian and Mopane Woodlands (AT0725); marginal occurrence in three other ecoregions.

Bioregions South Africa: N Lowveld (SVl), Mopane (SVmp) (Savanna Biome).

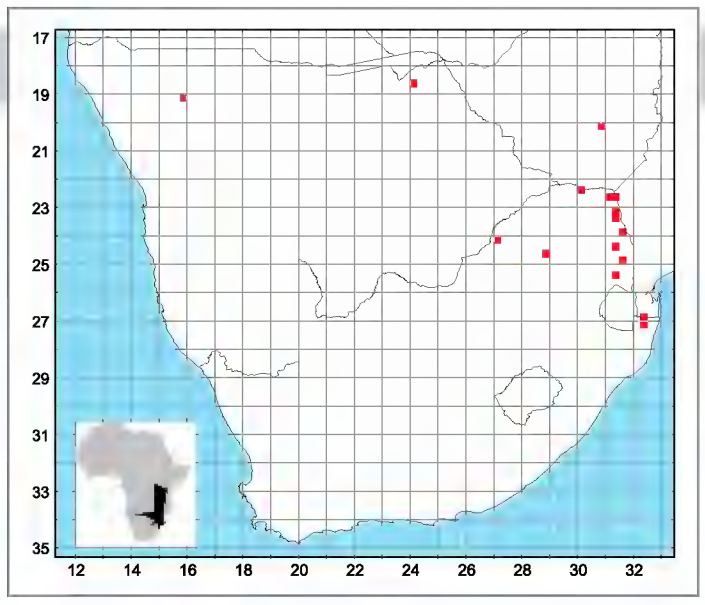
Assessment rationale: EOO = 2 951 525 km²; almost all South African records from the Kruger National Park; unclear if dominance of collection records from finer-grained soils in woodland on elephant dung represent a soil, vegetation and food type bias that would influence the AOO as regards habitat transformation and contraction in range of large monogastric herbivores and their coarse-fibred dung types; however, extremely widespread in hot savanna with most of South African range under protection; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; protected in various national parks: Kruger (South Africa), Gorongosa (Mozambique), South Luangwa (Zambia), Tsavo (Kenya).

Genus *Tragiscus* Klug, 1855

Type species and designation: *Tragiscus dimidiatus* Klug, 1855, by monotypy.
Synonyms: = *Deronitis* Arrow, 1933: Type species: *Deronitis epphipiatus* Arrow, 1933, by monotypy.
Last review: Janssens (1953).

Tragiscus Klug, 1855, is monotypic and endemic to the Afrotropical region where it shows endocoprid breeding habits within elephant and rhinoceros droppings. The single species shows a savanna distribution in the N of Namibia, Botswana and South Africa with a range extending into the E tropics.



Tragiscus dimidiatus

Klug, 1855

= *Deronitis ephippiatus* Arrow, 1933

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'Inhambane' [SE Mozambique coast]; *D. ephippiatus*: 'UGANDA: Katunguru, Kasinga Channel'.

Taxonomy: Accepted species.

Distribution: Dry to moist savanna from S to E Africa: South Africa, Namibia, Botswana, Zimbabwe, Mozambique, Kenya, Uganda.

Locality data (mean ± SD, range): Altitude: 471 ± 354, 0–1 259 m; annual rainfall: 602 ± 178, 328–1 136 mm; annual temperature (max. + min. /2): 22.4 ± 1.3, 19.6–25.2°C (N=24).

Habitat: No quantitative assessment; DBRU collection records from various soil types: sand (2), sandy loam (3), clay (1), all in open woodland (4).

Food types: No quantitative assessment; DBRU collection records all from monogastric herbivore dung: elephant (7), rhinoceros (1).

Temporal activity: Diurnal flight activity; recorded during the summer rainy season (Nov. to Apr.), but as a non-soil-tunnelling species constructing nest chambers within older droppings containing broods that are tended by the parent female during larval development, it probably remains active throughout the year as in other endocoprid taxa.

Ecoregions Namibia, Botswana, Zimbabwe: Angolan Mopane Woodlands (AT0702), Zambezian and Mopane Woodlands (AT0725), Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 2 192 930 km^2; AOO would be much smaller since all available records are from game reserves except for two on game farms (square-lipped (white) rhinoceros dung) and one in a hunting area (elephant dung); AOO reflects bias to dung of large monogastric herbivores whose ranges have now largely contracted to within the borders of protected areas; currently assessed as Least Concern (LC) since the EOO is large with records from various reserves.

Conservation measures: Conservation status of this species would depend on continuing protection of elephants and rhinoceros in dry savanna and would be improved by an investigation of soil and vegetation type associations as a possible further limitation on AOO; protected in various game reserves and national parks, including Kruger, Tembe (South Africa), Lake Mutirikwe (Zimbabwe) Chobe (Botswana), Etosha (Namibia), Gorongosa (Mozambique), Amboseli (Kenya).

TRIBE ONITINI

Castelnau, 1840

As Onitides; Type genus: *Onitis* Fabricius, 1798

The monophyletic, large-bodied, tunnelling tribe, Onitini, is represented across Afro-Eurasia although most of the genera are Afrotropical endemics. After the recent synonymy of *Janssensellus* Cambefort, 1976, with *Acanthonitis* Janssens, 1937 (Cambefort et al. 2010), the tribe now comprises 16 valid genera. These are endemic to the Afrotropical (13) or S Palaearctic regions (1) with the two most speciose genera shared between the Palaearctic, Oriental and Afrotropical regions.

Although primarily associated with savanna, grassland or winter rainfall shrublands, at least two monotypic genera are found in rainforest (*Allonitis* Janssens, 1936; *Lophodonitis* Janssens, 1938b) and one ranges into arid regions (*Cheironitis* van Lansberge, 1875b). There is also a strong trend to association with the dung of monogastric herbivores in all or some members of at least nine genera, which has implications for their conservation status given the restricted ranges now occupied by large indigenous monogastrics.

A total of 10 genera have been recorded for the Onitini in Botswana, Namibia and/or South Africa. Eight are species-poor whereas two are widespread in Afro-Eurasia and are species rich.

In southern Africa:

Two widespread Afro-Eurasian genera

(1) *Cheironitis* van Lansberge, 1875b: Five validated southern African species showing a bias to SW Arid regions (3) or dry savanna (2); some with a bias to monogastric herbivore dung.

(2) *Onitis* Fabricius, 1798: A total of 32 southern African species with distributions centred on savanna (20) upland grassland (6) savanna/grassland (2) or winter/bimodal rainfall shrublands (4). Close to half of the species may show a bias to the dung of monogastric herbivores.

Three Afrotropical genera with small savanna ranges

(3) *Anonychonitis* Janssens, 1950: Monotypic, monogastric dung specialist in one reserve on NE South African coastal hills.

(4) *Kolbeellus* Jacobson, 1906: Monotypic genus recently rediscovered in SE South Africa after a hiatus of at least 100 years.

(5) *Tropidonitis* Boheman, 1857: Monotypic, monogastric dung specialist on NE South African and SE Mozambique coastal sands.

Five Afrotropical genera with large savanna ranges and localised occurrence

(6) *Gilletellus* Janssens, 1937: One species recorded from buck pellets in N Namibia; possible wider range to South Africa depends on accuracy of identification.

(7) *Heteronitis* Gillet, 1911: One monogastric dung specialist ranging from S to E Africa.

(8) *Megalonitis* Janssens, 1937: One southern African monogastric herbivore dung specialist species.

(9) *Neonitis* Péringuey, 1901: Monotypic, monogastric dung specialist centred on savannas from N South Africa to E Democratic Republic of the Congo (DRC).

(10) *Platyonitis* Janssens, 1942: One species on moist deep sands of N Namibia and SW Angola; monogastric herbivore dung specialist.

Owing to various attributes: small ranges, dung type specialisation and/or infrequency of records, several monotypic genera or taxa of species-poor genera are assessed as threatened (NT: 1; VU: 2; DD/EN: 2).

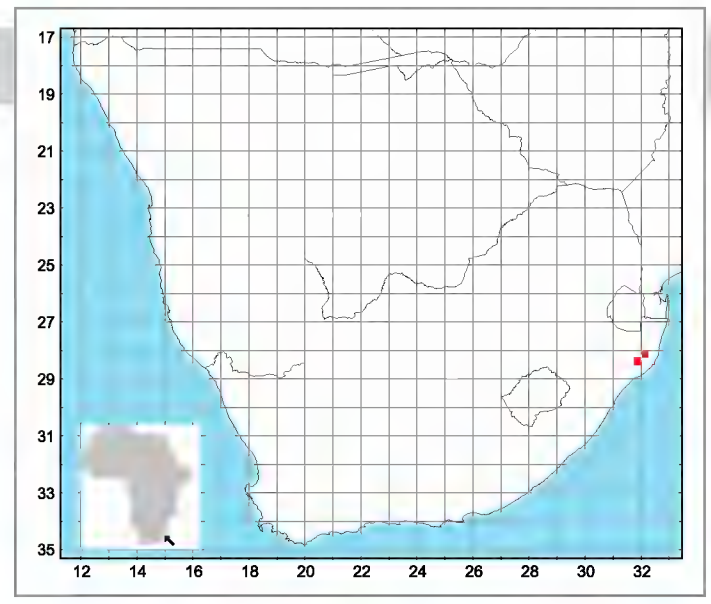
Genus *Anonychonitis* Janssens, 1950

Type species and designation: *Anonychonitis freyi* Janssens, 1950, by monotypy.
Synonyms: None.
Last review: Genus created by Janssens (1950).

Anonychonitis Janssens, 1950, is a monotypic genus recorded solely from rhinoceros dung in a small protected area of NE KwaZulu-Natal, South Africa. It is apparent that its conservation would be dependent on the continuing conservation of rhinoceros in Hluhluwe–iMfolozi Game Reserve in the face of an upsurge in poaching over the past few years.

Anonychonitis freyi

Janssens, 1950



No synonyms

Global: NT (see IUCN Red List – NT)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Zululand: Umfulozi' [Hluhluwe–iMfolozi Game Reserve, KwaZulu-Natal, South Africa].

Taxonomy: Accepted species; limited sexual dimorphism (head, prothoracic disc).

Distribution: Past EOO unknown; now restricted to lowland savanna in Hluhluwe–iMfolozi Game Reserve, KwaZulu-Natal, South Africa.

Locality data (mean ± SD, range): Altitude: 199 ± 65, 110–273 m; annual rainfall: 878 ± 22, 878–932 mm; annual temperature (max. + min. /2): 20.8 ± 0.3, 20.5–21.3°C (N=5).

Habitat: No quantitative assessment; DBRU collection records from clay (1) in open woodland (2), grassland clearing (1).

Food types: No quantitative assessment; all DBRU collection records from square-lipped (white) rhinoceros dung (4), which is dropped in middens; often found at the base of older droppings; cryptic owing to its habit of covering itself in dung fibres; constructs a single brood ovoid at the end of a tunnel in the soil.

Temporal activity: Diel flight periodicity unknown; active in the summer rainy season (Oct. to Mar.).

Bioregions South Africa: moist SE Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 960 km² (area, Hluhluwe–iMfolozi Game Reserve); AOO may be even smaller if soil and vegetation specialisations exist; known range entirely protected within a game reserve where it has been recorded only from the middens of square-lipped (white) rhinoceros, a monogastric herbivore species whose population density is being reduced by poaching throughout southern Africa, including Hluhluwe–iMfolozi where, recently (2014), there has been an increase in poaching; owing to very small EOO, AOO and potential poaching pressures on rhinoceros, *A. freyi* is currently assessed as Near Threatened (NT).

Conservation measures: Continued conservation of rhinoceros is essential for conservation of this species; a survey to precisely determine its ecological associations, AOO, and population density would be advisable, including an investigation to determine if it colonises the dung of elephants, which have been re-introduced into Hluhluwe–iMfolozi Game Reserve.

Genus *Cheironitis* van Lansberge, 1875b

Type species and designation: *Scarabaeus furcifer* Rossi, 1792, by subsequent designation (Arrow 1931).
Synonyms: = *Uposlotus* Costa, 1853, *nomen oblitum*: Type species: *Scarabaeus furcifer* Rossi, 1792, by subsequent designation (Arrow 1931).
= *Chironitis* van Lansberge *sensu* Janssens, 1937, misspelling of *Cheironitis*.
Last review: Entire genus reviewed by Janssens (1937); one species subsequently made a synonym of a species transferred from *Heteronitis* Gillet, 1911 (*C. audens* (Péringuey, 1901)); new Afrotropical species added by Janssens (1943), Balthasar (1963b), Ferreira (1976a); subtraction of two Afrotropical species into a new genus, *Pseudochironitis* Ferreira (1977).

Although often spelt as '*Chironitis*' following publications by Bedel (1892a) and Reitter (1893), Branco and Ziani (2005) made a case for van Lansberge's original spelling of *Cheironitis* as the valid spelling for this genus, citing rules of nomenclature in support. They also suggest that the senior synonym, *Uposlotus* Costa, 1853, should be considered invalidated as a *nomen oblitum* (= forgotten name) having been used as the genus name only once (Ádám 2003) since 1899.

A total of 22 species are currently placed in *Cheironitis.* These show distributions centred on drier regions of Afro-Eurasia. They are either endemic to the Palaearctic (10) and Afrotropical regions (10), or shared between the Afrotropical and Palaearctic (1), or Palaearctic and W Oriental regions (1).

In Africa, the general pattern of distribution is to the drier parts of the SW with a disjunction to the drier parts of the NE and W. Five species currently occur in southern Africa with another two remaining undescribed. Three described species show distributions centred on the SW arid late summer rainfall region with one also overlapping into the winter and bimodal rainfall regions during summer. One is distributed across Karoo, savanna and dry grassland. The fifth occurs in E dry savanna where it is associated with monogastric herbivore dung. Although species found in dry or arid areas are not threatened, possible effects of grassland modification and loss of zebra need to be investigated. Furthermore, adjustments to generic membership may be necessary for several taxa currently classified as *Cheironitis* species.

Cheironitis audens

(Péringuey, 1901)

= *Chironitis damarensis* Felsche, 1907

Global: LC (see IUCN Red List – LC)
Endemic: RSA, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Onitis audens*: 'Cape Colony (Prieska)' [Prieska, Northern Cape, South Africa]; *C. damarensis*: 'Kubub, D. S.-W. Afrika' [?river or farm in Namibia].

Taxonomy: Accepted species; some sexual dimorphism (legs, prosternum).

Distribution: Arid late summer rainfall region with populations disjunct in South Africa / S Namibia and N Namibia Plateau; disjunction does not appear to be a collection artefact.

Locality data (mean ± SD, range): Altitude: 1 100 ± 214, 608–1 855 m; annual rainfall: 241 ± 74, 118–455 mm; annual temperature (max. + min. /2): 17.9 ± 2.0, 11.9–23.0°C (N=105).

Habitat: No formal quantitative assessment; soil generalisation shown in Northern Cape: sand (3.9), sandy loam (3.7), sandy clay loam (2.7); sampled equally in Upper Karoo and Bushmanland (0.2/trap), rare in SW Kalahari (0.001); largely supported by DBRU collection records on sand (8), sandy loam (8), sandy clay loam (11) primarily in scrub/shrubland (11) and open woodland (6), few in pasture (2).

Food types: No quantitative assessment; DBRU collection records from ruminant: cattle (17), wildebeest (2) and monogastric herbivore dung: zebra (4), horse (2), donkey (2).

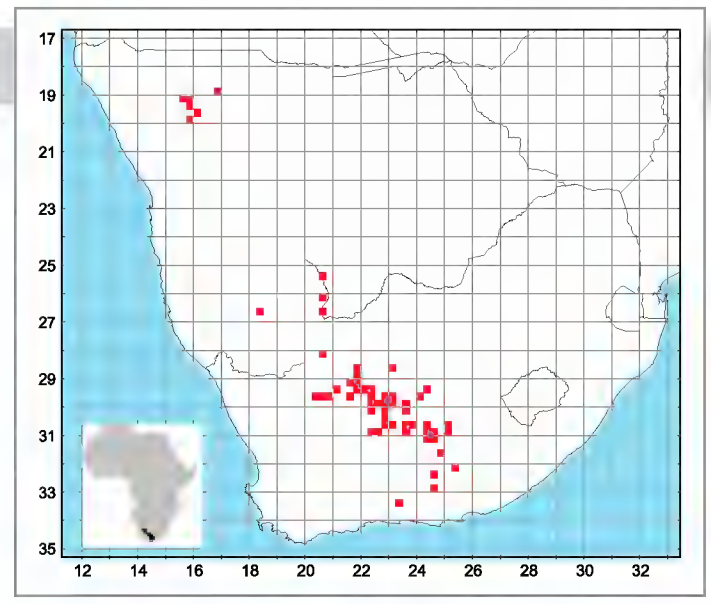
Temporal activity: Diurnal flight activity in the late summer rainy season (Dec. to Apr.).

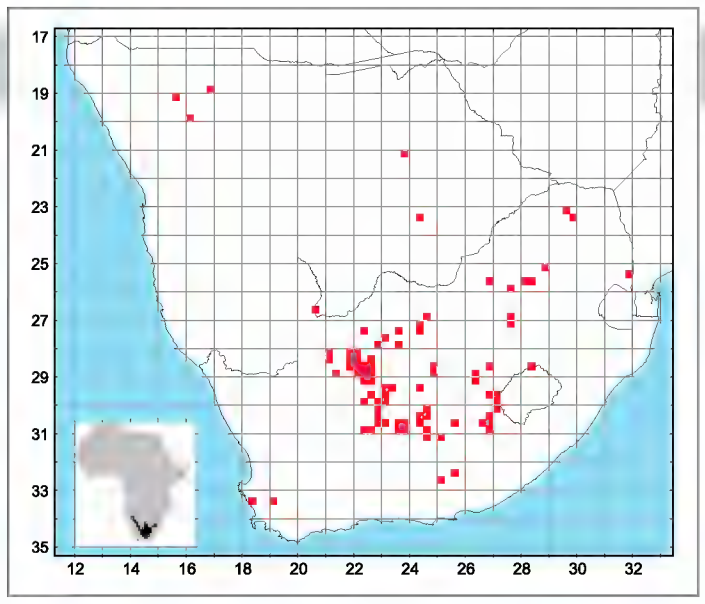
Ecoregions Namibia: In S: Nama Karoo (AT1314); in N: restricted to Angolan Mopane Woodlands (AT0702).

Bioregions South Africa: Upper Karoo (Nku), Bushmanland (NKb) (Nama Karoo Biome); marginal in four other bioregions.

Assessment rationale: EOO = 208 390 km² (assumes continuous range); widespread across arid regions used primarily for the grazing of livestock; readily attracted to the dung of both ruminant and monogastric herbivores on farms where there is little transformation (NKb, NKu); assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by further quantitative data on ecological associations despite observed, large, little-transformed range and association with dung of farm livestock; a survey to demonstrate a truly disjunct or continuous range would also be useful; little protection across main South African range; however, protected in Etosha National Park (Namibia).





Cheironitis hoplosternus

(Harold, 1868)

No synonyms

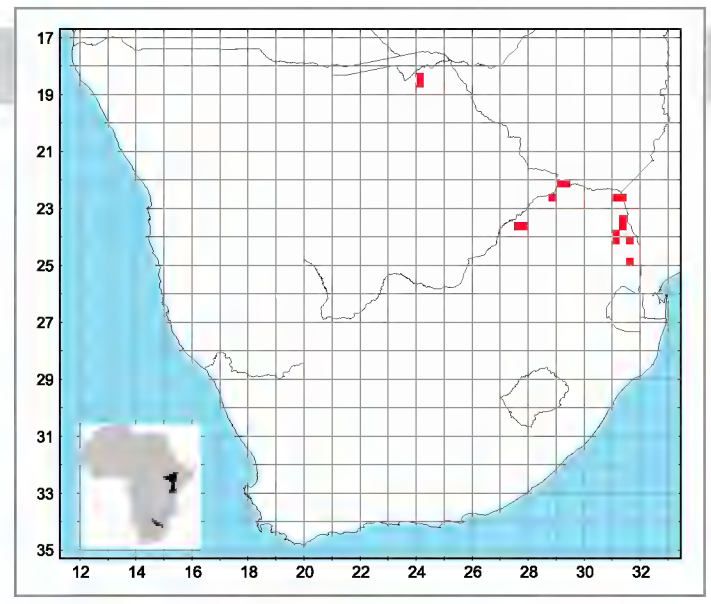
Global: LC
Endemic: RSA, Botswana, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Onitis hoplosternus* 'Afric. austr. inter.' [interior of southern Africa].
Taxonomy: Accepted species; some sexual dimorphism (legs, prosternum).
Distribution: Dry W uplands, central South Africa encompassing: SE Kalahari, NE Karoo, W Highveld grasslands; also sporadic marginal records from dry savanna: South Africa, Botswana, N Namibia Plateau.
Locality data (mean ± SD, range): Altitude: 1 187 ± 260, 62–1 964 m; annual rainfall: 353 ± 153, 172–815 mm; annual temperature (max. + min. /2): 17.7 ± 2.0, 12.5–22.9°C (N=138).
Habitat: No adequate quantitative assessment; in Northern Cape: primarily sampled from SW Kalahari (0.7/trap), less in Upper Karoo (0.4) and arid Bushmanland (0.002); DBRU collection records from a range of soil and vegetation types: clay (3), sandy clay loam (5), sandy loam (13), sand (12), on pasture/grassland (15), scrub/shrubland (6) and open woodland (4); also fallow crop fields (2).
Food types: No quantitative assessment; DBRU collection records primarily from dung of ruminant herbivores: cattle (33); but also monogastric herbivore dung: horse (3), zebra (2), donkey (1); trapped to pig dung in Botswana (1 individual).
Temporal activity: Diurnal flight activity in the summer rainy season (Oct. to Apr.)
Ecoregions Namibia, Botswana Kalahari Xeric Savanna (AT1309), Kalahari Acacia-Baikiaea Woodlands (AT0709), Angolan Mopane Woodlands (AT0726).
Bioregions South Africa: N Upper Karoo (NKu) (Nama Karoo Biome); East Kalahari Bushveld (SVk), S Central Bushveld (SVcb) (Savanna Biome); also Dry Highveld Grassland (Gh) (Grassland Biome); sporadic occurrence in five other bioregions across four biomes.
Assessment rationale: EOO = 651 685 km^2; main SW range little transformed (0–2%; SVk, NKu); main NE range more transformed (10–63%; SVk, Gh); isolated records in SW Cape pastures may be a response to transformation of natural shrubland; widespread and readily attracted to the dung of domestic livestock in farm rangeland; assessed as Least Concern (LC).
Conservation measures: Assessment of conservation status would benefit from quantitative data on ecological associations and population density as there are currently few records from reserves in South Africa; protected in Etosha National Park (Namibia).

Cheironitis imitator

(Balthasar, 1963b)



No synonyms

Global: DD (see IUCN Red List as *C. indicus* – DD)

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Chironitis imitator*: Holotype: 'Sudan (Mongalla, Lado)' [South Sudan: Mongalla, Lado].

Taxonomy: Accepted species, but southern African individuals need to be compared with type material from NE Africa to validate their identity as *C. imitator* rather than an extremely close undescribed relative; from the descriptions of the prosternal spurs, it seems that Balthasar (1963b) compared *C. imitator* with the true *C. indicus* from arid SW Africa (see species page for *C. indicus* van Lansberge, 1875b) rather than with these southern African individuals treated here as *C. imitator*; some sexual dimorphism (legs, prosternum).

Distribution: In southern Africa: shows an apparent disjunct pattern in two lowland centres; Savuti, Okavango Delta, Botswana and NE lowlands plus Limpopo Valley, South Africa; the major disjunction in overall species range between S and NE plus E Africa may or may not indicate two closely related species.

Locality data (mean ± SD, range): Altitude: 541 ± 251, 278–1 000 m; annual rainfall: 486 ± 104, 309–655 mm; annual temperature (max. + min. /2): 22.3 ± 0.6, 21.3–23.1°C (N=16).

Habitat: No quantitative data; DBRU collection records from various soil types: sand (2), sandy loam (3), sandy clay loam (1) entirely in open woodland (4).

Food types: No adequate quantitative data; at Phalaborwa: sampled to pig dung (2); however, DBRU collection records from southern Africa indicate a bias to coarse-fibred dung of monogastric herbivores: elephant (5), donkey (3) plus cattle dung (1); many E African records for *C. imitator* also from elephant and zebra dung.

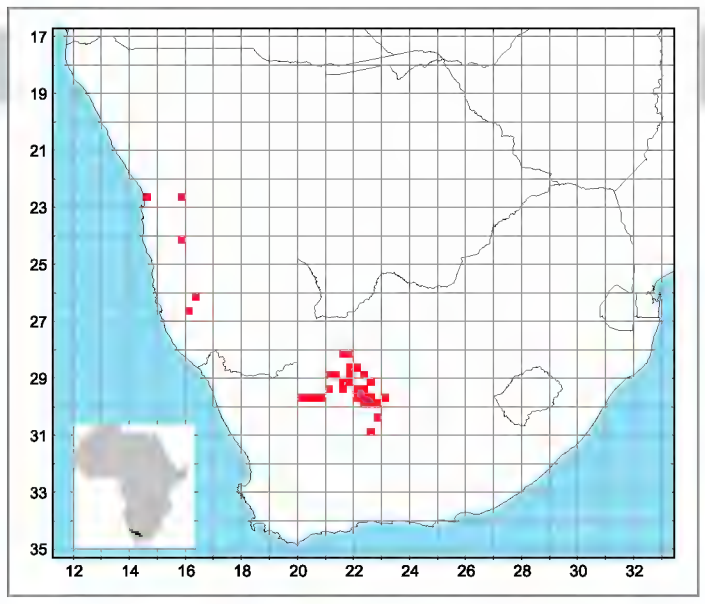
Temporal activity: Diurnal flight activity in the summer rainy season (Nov. to Mar.).

Ecoregions Botswana: Zambezian and Mopane Woodlands (AT0725).

Bioregions South Africa: Dry lowlands of Central Bushveld (SVcb), Lowveld (SVl) and especially Mopane (SVmp) (Savanna Biome).

Assessment rationale: EOO = 669 950 km^2 (gross estimate); AOO would be smaller if disjunct pattern is real rather than a collection artefact; disjunction possibly related to dung type association reflecting range contraction onto game reserves for indigenous monogastric herbivores and scattered occurrence of domestic monogastric herbivores in farmland; this could represent a threat over most of the potential EOO in southern Africa; owing to limited ecological data, assessed as Data Deficient (DD).

Conservation measures: Before conservation status may be assessed, taxonomic uncertainties need to be resolved regarding identity as *C. imitator* Balthasar, 1963, or a close undescribed relative; a survey to determine the full EOO and AOO is also required as well as quantitative data on ecological associations; protected in two national parks, Kruger (South Africa), Chobe (Botswana) that support large populations of elephants.



Cheironitis indicus

van Lansberge, 1875b

No synonyms

Gloal: LC
Endemic: RSA, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: Cited as 'Inde en deçà du Gange. Arabie' [India 'below' the Ganges; Arabia], but see Taxonomy section.

Taxonomy: Accepted species, but type unknown (Janssens, 1937); Janssens (1937) states that material from Windhoek, Namibia, in Gillet's collection corresponds to van Lansberge's original description, whereas it does not match Arrow's (1931) description of material from India [and Karachi, Pakistan] cited as *C. indicus* van Lansberge, 1875b; this Indian material is now classified under the *nom nov.* of *C. arrowi* (Janssens, 1937); also see the species account for *C. imitator* Balthasar, 1963b; some sexual dimorphism (legs, prosternum).

Distribution: Arid SW summer rainfall region from Bushmanland, South Africa, N along and below the W escarpment as far N as Windhoek, Namibia.

Locality data (mean ± SD, range): Altitude: 1 028 ± 203, 58–1 762 m; annual rainfall: 196 ± 47, 14–255 mm; annual temperature (max. + min. /2): 18.5 ± 1.4, 13.0–20.3°C (N=61).

Habitat: In Northern Cape: recorded to composite sheep/cattle baits in low abundance (0.3–0.4/trap per study site) in 70 out of 406 sites; Bushmanland (27 sites), Upper Karoo extension (27), SW Kalahari (14), Upper Karoo (2); frequency of records on deep sand, loamy or rocky sand sites (47) greater than sandy loam (22) or sandy clay loam (1); limited DBRU collection records entirely on deep sand (4) in scrub (2) or open woodland (2).

Food types: No quantitative assessment; limited DBRU collection records on dung of horse (1), donkey (1), cattle (1).

Temporal activity: Diurnal flight activity during the late summer rainy season (Feb., Mar.).

Ecoregions Namibia: S Namibian Savanna Woodlands (AT1316), Namib Desert (AT1315).

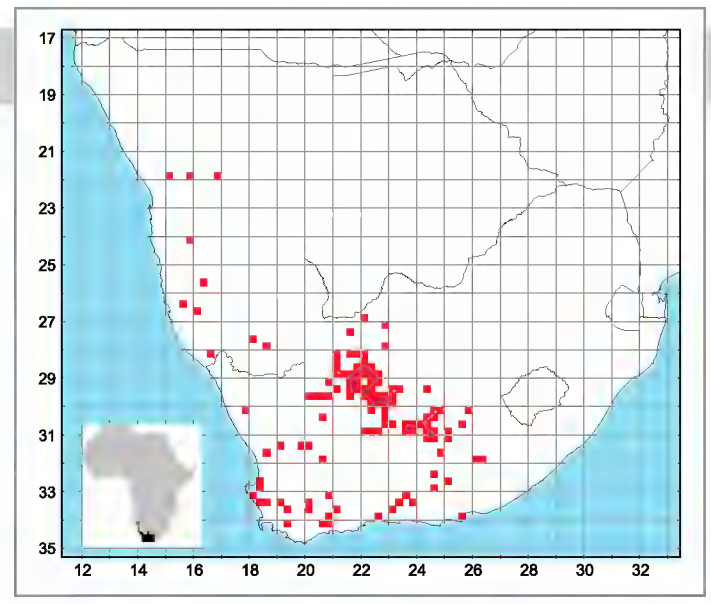
Bioregions South Africa: N Bushmanland (NKb), marginal in W Upper Karoo (NKu).

Assessment rationale: EOO = 113 785 km²; centred in an area that has undergone little habitat transformation and is used primarily for grazing of farm livestock; not considered to face current threats as it has been widely recorded in dung on farms in the Northern Cape; therefore, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative assessment of ecological associations, particularly as existing data suggest a bias to sandy soils; high spatial frequency, but low abundance in samples, need to be investigated as they may result from bias to monogastric herbivore dung like some relatives; may be protected in parts of the Namib/Naukluft National Park, Namibia.

Cheironitis scabrosus

(Fabricius, 1776)



No synonyms

Global: LC (see IUCN Red List – LC)
Endemic: RSA, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Scarabaeus scabrosus*: 'Surinami' [Surinam – undoubtedly an error].
Taxonomy: Accepted species some sexual dimorphism (legs, prosternum).
Distribution: Dry to arid areas in the late summer, winter and bimodal rainfall regions of SW South Africa and SW Namibia.
Locality data (mean ± SD, range): Altitude: 1 017 ± 321, 16–1 855 m; annual rainfall: 244 ± 81, 29–509 mm; annual temperature (max. + min. /2): 17.6 ± 1.8, 11.9–20.5°C (N=242).
Habitat: No quantitative soil type assessment; in the SW on deep sands of West Coast National Park: primarily sampled in pasture (46) following clearance of natural shrubland, few in natural shrubland (4); in the NE, primarily sampled from scrub in the Upper Karoo (5.6/trap), less in arid Bushmanland (1.0) and deep sands of SW Kalahari (0.2); DBRU collection records from clay (2), sandy clay loam (15), sandy loam (14), sand (11) in shrubland (4), scrub (19), pasture/grassland (9) and crop fields (3).
Food types: No quantitative assessment; DBRU collection records dominated by ruminant herbivore dung: cattle (42), sheep (1); also monogastric herbivore dung: horse (4)
Temporal activity: Diurnal flight activity during the summer rainy season to the NE (Sept.–Apr.); similar seasonality during the dry mid-summer of the winter rainfall region to the SW (Nov.–Feb.) peaking in Dec. in West Coast National Park.
Ecoregions Namibia: S Namibian Savanna Woodlands (AT1316), Nama Karoo (AT1314), Succulent Karoo (AT1322).
Bioregions South Africa: Upper Karoo (NKu), Bushmanland (NKb) (Nama Karoo Biome); also in Succulent Karoo, Fynbos (FF, FR) and SW Savanna Biomes.
Assessment rationale: EOO = 478 375 km^2; widespread; readily attracted to the dung of domestic livestock in rangeland; little transformation in scrub habitats in the arid NE of its range (0–2%; NK); to the SW where transformation is high (5–80%; FF, FR), dry mid-summer activity and much greater abundance in pastures may indicate range (or at least population) expansion in response to clearance of indigenous shrubland; assessed as Least Concern (LC).
Conservation measures: Assessment of conservation status would be improved by further quantitative data on ecological associations; few records from protected areas, but widespread on domestic dung types in farm rangeland and adaptable to transformation in the SW; despite widespread occurrence and abundance, no current records from protected areas.

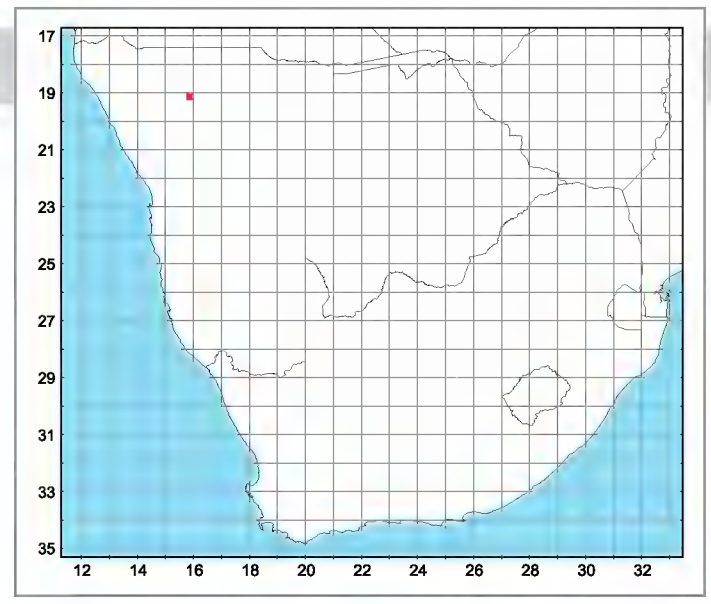
Genus *Gilletellus* Janssens, 1937

Type species and designation: *Onitis porculus* Boheman, 1857, by subsequent designation (Janssens 1937).
Synonyms: None.
Last review: Entire genus reviewed by Janssens (1937).

Gilletellus Janssens, 1937, is represented by just two S Afrotropical species described from inexact localities presumed to be in South Africa and possibly Mozambique, ('Zambèze' Province of Mozambique or elsewhere along the Zambezi River?). Genus poorly known due to extremely infrequent records with little precise information. Assessed as Data Deficient (DD), but only a single specimen known to have been recorded in the past 40 years.

Gilletellus porculus

(Boheman, 1857)



No synonyms

Global: DD
Endemic: ?RSA, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Onitis porculus*: 'Caffraria interiore' [inexact, interior of southern or South Africa].

Taxonomy: Accepted species; limited sexual dimorphism (legs); species identification requires validation.

Distribution: A single record from the dry W of Etosha National Park suggests that the inexact type locality may refer to the interior of southern Africa within the arid late summer rainfall region, but this is speculative given its extreme rarity in collections.

Locality data (average): Altitude: 1 156 m; annual rainfall: 391 mm; annual temperature (max. + min. /2): 22.2°C (N=1).

Habitat: No quantitative assessment; a single DBRU collection record from sandy clay loam in scrub.

Food types: No quantitative assessment; a single DBRU collection record from springbok pellets.

Temporal activity: Unknown.

Ecoregions Namibia: Angolan Mopane Woodlands (AT0702).

Assessment rationale: EOO impossible to determine; a single specimen recorded on springbok dung may or may not be indicative of dung type specialisation in this excessively rare species; must be assessed as Data Deficient (DD) because of the paucity of data, but its apparent rarity is a cause for great concern; the single record would currently justify Endangered (EN) or even Critically Endangered (CR) status.

Conservation measures: A survey from dry to arid savanna is required to determine the local EOO, ecological associations, AOO and population density of *G. porculus* in W Etosha National Park where it is under protection; such a survey would provide insights on how to assess its conservation status across a potentially much larger EOO and AOO, possibly southwards to South Africa.

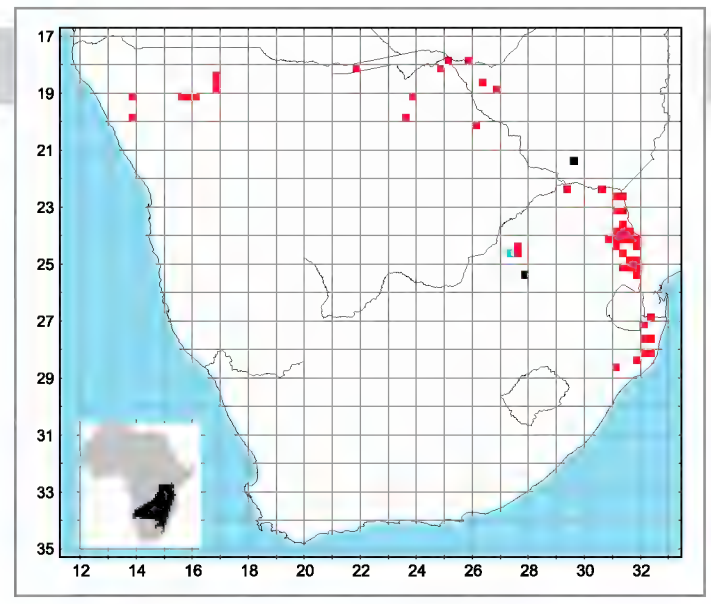
Genus *Heteronitis* Gillet, 1911

Type species and designation: *Onitis tridens* Castelnau, 1840, by subsequent designation (Janssens 1937).
Synonyms: None.
Last review: Entire genus reviewed by Janssens (1937) with subsequent removal of one species to *Cheironitis* van Lansberge, 1875b (see *C. audens* (Péringuey, 1901)).

Heteronitis Gillet, 1911, currently comprises five Afrotropical species found in savannas from S to E to W Africa where they are, apparently, associated primarily with elephant dung. Most species ranges are centred in E (2) or W Africa (2). Only a single species shows a range from southern to E Africa; largely restricted to reserves in southern Africa, but assessed as Least Concern (LC) on basis of wide EOO and protection in many reserves.

Heteronitis castelnaui

(Harold, 1862)



No synonyms

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Onitis castelnaui*: 'Zanzibar' [Tanzania].

Taxonomy: Accepted species; sexually dimorphic (head, prothoracic disc, legs), prominence of characters varies with body size.

Distribution: S to E African savanna; patchy occurrence due to dung type specialisation; primarily centred on game reserves: N South Africa, N Namibia, N Botswana, Zimbabwe, Mozambique, Angola, Zambia, Tanzania, Kenya; also reported from Democratic Republic of the Congo (DRC), Rwanda.

Locality data (mean ± SD, range): Altitude: 565 ± 394, 55–1 448 m; annual rainfall: 605 ± 168, 172–1 136 mm; annual temperature (max. + min. /2): 22.0 ± 1.7, 15.7–25.9°C (N=74).

Habitat: No quantitative assessment; DBRU collection records indicate a bias to finer-grained soils: sandy clay loam (5), sandy loam (11), sand (5), and woody vegetation: dry forest (1), open shrub/woodland (14), scrub (3), grassland (2).

Food types: No quantitative assessment; DBRU collection records dominated by monogastric dung types: elephant (25), hooked-lipped (black) (2) and square-lipped (white) (4) rhinoceros, zebra (3), horse (1), donkey (1); also warthog (1); few on ruminant dung types: cattle (3).

Temporal activity: Diel flight activity in fading light and crepuscular darkness (late afternoon to dusk or dawn to early morning) (Caveney et al. 1989) primarily in the summer rainy season (Oct. to May); attracted to light.

Ecoregions Namibia, Botswana, Zimbabwe: Angolan Mopane Woodlands (AT0702), N Namibian Savanna Woodlands (AT1316), Zambezian Baikiaea Woodlands (A0726), Zambezian and Mopane Woodlands (AT0725), Kalahari Acacia-Baikiaea Woodlands (AT0709), Southern African Bushveld (AT0717).

Bioregions South Africa: Central Bushveld (SVcb), Lowveld (SVl), Mopane (SVmp) (Savanna Biome).

Assessment rationale: EOO = 3 997 830 km² (gross estimate); AOO very much smaller due to dung, and possible soil and vegetation specialisation; 82% (N=42/51) of DBRU collection records (1971–1986) from proclaimed reserves; such concentration of recent records indicates a clear effect of range contraction by large monogastric herbivores; single records in areas distant from reserves (black squares) suggest very low density relict populations (Buffelsdoorn in South Africa; West Nicholson in Zimbabwe); greater numbers have been recorded from areas where rhinoceros have been re-introduced, e.g. reserves near Thabazimbi, South Africa (blue square); because of wide range and protection in many reserves, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, including population density both inside and outside of reserves; conservation dependent on continuing protection of indigenous monogastric herbivores, particularly elephant and rhinoceros; currently protected in many national parks and game reserves: Hluhluwe–iMfolozi, Kruger (South Africa), Hwange (Zimbabwe), Etosha (Namibia), Serengeti, Manyara (Tanzania), Masai Mara, Meru (Kenya).

Genus *Kolbeellus* Jacobson, 1906

Type species and designation: *Tapeinopterus ateuchoides* van Lansberge, 1875b, by subsequent designation (Janssens 1937).

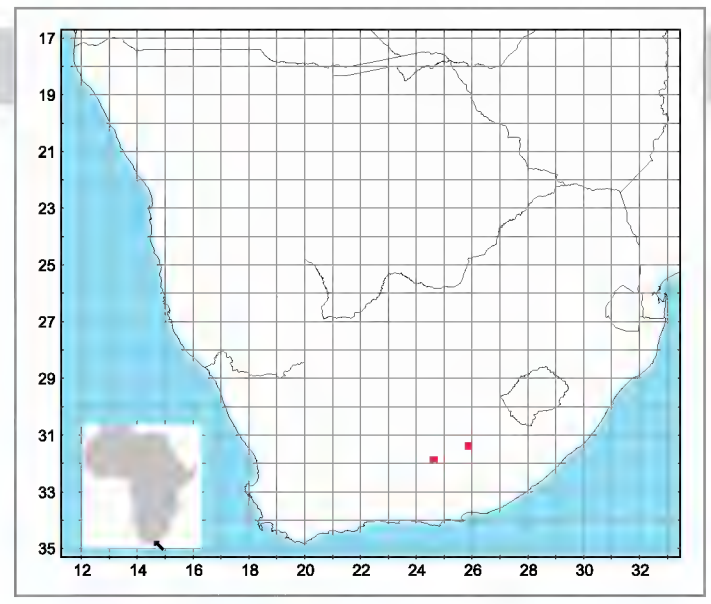
Synonyms: = *Tapeinopterus* van Lansberge, 1875b: Type species: *Tapeinopterus ateuchoides* van Lansberge, 1875b, by monotypy.

Last review: Entire genus reviewed by Janssens (1937).

Kolbeellus Jacobson, 1906, is a *nom nov*. for *Tapeinopterus* van Lansberge, 1875b, which is a previously occupied name for a genus of Carabidae. *Kolbeellus* is monotypic, exceedingly rare, occupying a small, ill-defined range in the Eastern Cape, South Africa, where protection of the genus is urgently required.

Kolbeellus ateuchoides

(van Lansberge, 1875b)



Global: DD (see IUCN Red List – DD)
Endemic: RSA

| J | A | S | O | N | D | J | F | M | A | M | J |

Type locality: As *Tapeinopterus ateuchoides*: 'Afrique austral' [southern Africa].

Taxonomy: Accepted species; *Kolbeellus ateuchoides* (van Lansberge, 1875b) is a *nom nov.* for *Tapeinopterus ateuchoides* van Lansberge, 1875b.

Distribution: Dry upland localities, at the SE edge of the Upper Karoo, Eastern Cape, South Africa.

Locality data (mean ± SD, range): Altitude: 1 890 ± 735, 1 371–2 410 m; annual rainfall: 429 ± 21, 414–443 mm; annual temperature (max. + min. /2): 11.9 ± 4.2, 8.9–14.9°C (N=2).

Habitat: No quantitative assessment; unknown.

Food types: No quantitative assessment; unknown.

Temporal activity: Unknown.

Bioregions South Africa: Upper Karoo Hardeveld (NKu 2), Eastern Upper Karoo (NKu 4) (Upper Karoo Bioregion, Nama Karoo Biome); both localities very close to outliers of Karoo Escarpment Grassland (Gh 1) (Dry Highveld Grassland Bioregion, Grassland Biome).

Assessment rationale: EOO = 1 395 km^2; known only by the holotype male recorded in the 19th century and a few specimens recently recorded in the Eastern Cape, South Africa (2004); the hiatus between collections suggest genuine rarity, this may be related to range contraction of monogastic herbivores, such as elephant and zebra, since many species-poor onitine genera are specialists on their coarse-fibred dung; however, this possibility currently remains speculative; owing to paucity of data, assessed as Data Deficient (DD), but known distribution of < 5 000 km^2 at < five known locations qualifies for Endangered status (EN).

Conservation measures: A quantitative survey is required to determine the EOO, AOO and ecological associations; a study at known localities is required to determine if specialist dung type associations might be the reason for rare occurrence in drier upland islands at SE edge of the Upper Karoo; not currently known from any protected area.

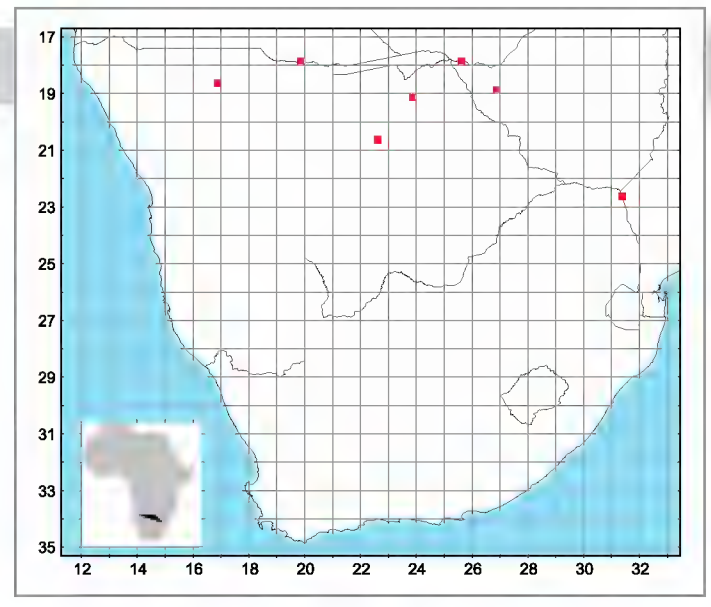
Genus *Megalonitis* Janssens, 1937

Type species and designation: *Onitis gigas* Bertolini, 1855, by subsequent designation (Janssens 1937).
Synonyms: None.
Last review: Genus created and reviewed by Janssens (1937).

Megalonitis Janssens, 1937, currently comprises two species found in dry savanna of southern Africa where they are probably associated with elephant dung. Despite the wide range, *Megalonitis* species are rarely recorded and then only in game reserves, hence the assessment of Data Deficient (DD). Janssens (1937) did not see the type species of the genus (*M. gigas* (Bertolini, 1855)) and notes that differences to *M. bohemani* (van Lansberge, 1875b) may merely represent morphological variation associated with body size. If so, *M. bohemani* would become a junior synonym.

Megalonitis bohemani

(van Lansberge, 1875b)



No synonyms

Global: DD (see IUCN Red List – DD)

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Onitis bohemanni*: 'Caffrerie intérieure (N'Gami)' [interior of SE Africa = Lake Ngami, Botswana].

Taxonomy: Accepted species; however, comparison of type material is necessary to determine if *M. bohemani* might be a junior synonym of *M. gigas* (Bertolini, 1855), described from Mozambique; limited sexual dimorphism (legs, head).

Distribution: Fragmented range in dry southern African savanna: N Namibia, N Botswana, Zimbabwe, NE South Africa.

Locality data (mean ± SD, range): Altitude: 928 ± 241, 429–1 127 m; annual rainfall: 528 ± 87, 414–659 mm; annual temperature (max. + min. /2): 22.4 ± 0.6, 21.1–23.1°C (N=7).

Habitat: No quantitative assessment; DBRU collection records from sand (1), sandy loam (2), sandy clay loam (1) in open woodland (2), grassland (1).

Food types: No quantitative assessment; DBRU collection records entirely from monogastric herbivore dung: elephant (5).

Temporal activity: Flight activity during darkness in the summer rainy season (Nov. to Apr.); attracted to light.

Ecoregions Namibia, Botswana, Zimbabwe: Angolan Mopane Woodlands (AT0702), Zambezian Baikiaea Woodlands (AT0726), Zambezian and Mopane Woodlands (AT0725), Kalahari Acacia-Baikiaea Woodlands (AT0709).

Bioregions South Africa: Mopane (SVmp) (Savanna Biome).

Assessment rationale: EOO = 317 740 km^2 (?underestimated); AOO much smaller; entirely recorded from game reserves, presumably due to specialisation on the dung of elephants whose ranges are now fragmented and restricted; widespread, but rare, suggesting low population density even in game parks; assessed as Data Deficient (DD) because of limited data although may deserve a threat category despite wide range.

Conservation measures: Assessment of conservation status will only be possible once a quantitative survey has determined its ecological associations, AOO and population density; limited available data suggest that continuing protection of elephants in dry savanna reserves of southern Africa is essential for the conservation of this species; protected in various national parks and game reserves: Etosha (Namibia), Moremi (Botswana), Victoria Falls, Hwange (Zimbabwe), Kruger (South Africa).

Genus *Neonitis* Péringuey, 1901

Type species and designation: *Neonitis porculus* (Boheman) *sensu* Péringuey, 1901, by monotypy.
Synonyms: None.
Last review: Entire genus reviewed by Cambefort et al. (2010).

Neonitis Péringuey, 1901, was described to accommodate a single misidentified species (*Neonitis porculus* (Boheman) *sensu* Péringuey, 1901, ≠ *Gilletellus porculus* (Boheman, 1857)). Gillet subsequently recognised the error and renamed the species *Neonitis rhodesiae* Gillet, 1918, although Cambefort et al. (2010), thereafter, synonymised it with *Neonitis nigritiae* Gillet, 1918. Two new species of '*Neonitis*' described by Cambefort (1995) are now transferred by Cambefort et al. (2010) to the genus, *Acanthonitis* Janssens, 1937, with its synonym *Janssensellus* Cambefort, 1975. *Neonitis* now comprises a single, rarely recorded, SE African species. It has been recorded from elephant dung in South Africa whereas Cambefort et al. (2010) record diurnal activity by the species in Tanzania.

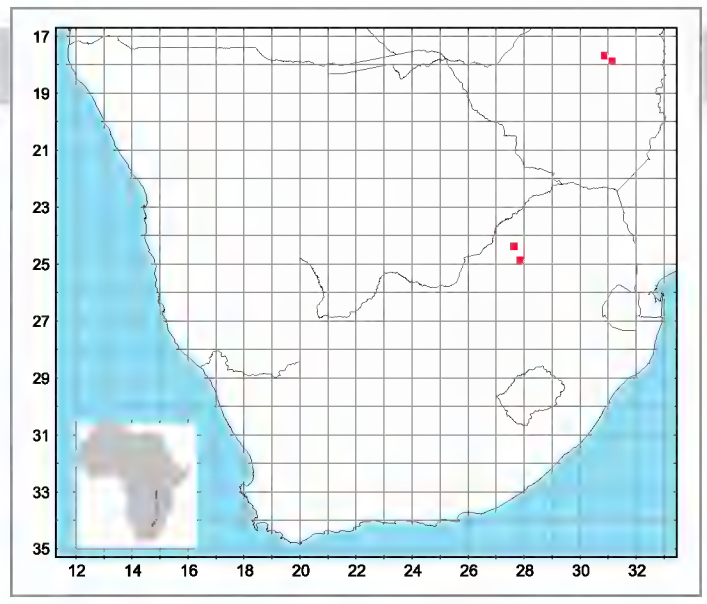
Neonitis nigritiae

Gillet, 1918

= *Neonitis rhodesiae* Gillet, 1918
= *Neonitis porculus* (Boheman, 1857) *sensu* Péringuey, 1901

Global: DD

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: *N. nigritiae*: 'Afrique orientale: Ile de Wau dans le lac Kivu' [?Isle of Idjwi, Lake Kivu, Congo DRC]; *N. rhodesiae*, *nom nov.* for *N. porculus sensu* Péringuey: 'Southern Rhodesia (Salisbury, Mazoe)' [Zimbabwe: Harare, Mazoe].

Taxonomy: Accepted, sexually dimorphic species (head, legs); *Neonits porculus* (Boheman) *sensu* Péringuey (1901) was confused with *Onitis porculus* Boheman, 1857 (type loc. 'Caffraria interiore') (now *Gilletellus porculus* (Boheman)); Gillet (1918) renamed *Neonitis porculus* as *N. rhodesiae*; southern African *N. rhodesiae* was recently (2010) synonymised with East African *N. nigritiae*; female specimen from South Africa illustrated here requires validation as *N. rhodesiae* / *N. nigritiae*.

Distribution: Difficult to assess owing to rarity in collections, but known from moist savanna from SE to E Africa; type localities in E Democratic Republic of the Congo (DRC) and N Zimbabwe; also, recently cited from Tanzania (2010); new (2009) record from NW South Africa requires validation; citation from Free State, South Africa, also requires validation.

Locality data (mean ± SD, range): Altitude: 1 355 ± 107, 1 204–1 448 m; annual rainfall: 748 ± 117, 627–861 mm; annual temperature (max. + min. /2): 18.7 ± 0.5, 18.2–19.4°C (N=4).

Habitat: No quantitative assessment; southern African savanna presumably differs from tropical habitat on islands in Lake Kivu.

Food types: No quantitative assessment; unknown, but suspected to be a monogastric dung specialist.

Temporal activity: Diurnal flight activity during the summer rainy season (Dec.).

Ecoregions Zimbabwe: Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Close to Waterberg in Central Bushveld (SVcb) (Savanna Biome).

Assessment rationale: EOO = 123 785 km^2 (underestimated); AOO undoubtedly much smaller; rarity in collections probably related to extremely low population density with specialisation to the coarse-fibred dung of large monogastric herbivores whose ranges have now largely contracted within the boundaries of game reserves; after revision (2010), *Neonitis* becomes a monotypic genus; poorly known, so assessed as Data Deficient (DD); however, rarity and probable small AOO suggests it deserves some level of threat category despite a large EOO.

Conservation measures: A quantitative survey focused on game reserves is required to determine the EOO, AOO, ecological associations and population density; unknown whether or not it is adequately protected in game reserves; record from Mabalingwe Game Reserve, South Africa remains unvalidated; known older records from type localities lie outside of protected areas.

Genus *Onitis* Fabricius, 1798

Type species and designation: *Scarabaeus sphinx* Olivier, 1789, by subsequent designation (Latreille 1810).
Synonyms: None.
Last review: All Afrotropical species reviewed by Ferreira (1978); further new Afrotropical species described, subsequently (Houston 1983; Cambefort 1984; Davis 1986; Moretto 2010), plus reviews and additions to species groups XI (Josso 2012) and XIII (Moretto 2007).

The long-established genus, *Onitis* Fabricius, shows a distribution centred on the tropics and warm temperate regions of Afro-Eurasia. It is currently divided into 19 species groups comprising 170 species. These are, essentially, endemic to the Palaearctic (10), Oriental (24) and Afrotropical regions (134) with two shared between the Afrotropics and Palaearctic.

Eight groups and 32 species of *Onitis* are represented within South Africa, Botswana and Namibia. Some species show specialisations that may influence their conservation status. In particular, associations with the dung of range-restricted monogastric herbivore influences the AOO of about 14 species comprising some or all species in six of the eight groups. AOO is also influenced by bias to particular soil types (at least some species of six groups) or to woody vegetation cover (particularly Group XVII).

Onitis species are relatively large bodied and construct broods at the ends of tunnels leading from under droppings. These may comprise single brood ovoids at the branched tips of the tunnel, separated by soil (Group XVII) or clustered together (some Group III) (Edwards & Aschenborn 1987). Or, they may comprise brood sausages with eggs laid at intervals, either along a single sausage (Group XVIII) or along multiple sausages clustered together at the branched tips of the tunnel (some Group III, Group VII). This nest architecture requires large amounts of dung. Therefore, they are found primarily in moister regions that support large herbivores dropping large amounts of dung. Few species occur where such large herbivores do not occur naturally, such as particularly arid regions or the central Kalahari where surface water is scarce.

Onitis species are macropterous flying during darkness at dusk, dusk and dawn, or dusk, night and dawn, although some species at the more temperate northernmost and southernmost limits of their latitudinal range are day fliers (see Group VII). Of the 32 species in southern Africa, 24 are restricted to southern Africa with only eight showing larger, more widespread ranges into the tropics. In southern Africa, most species show northerly ranges centred on savanna (20) either in the east (12), the west (5) or both (3). Others are centred in savanna and Highveld Grassland (2), Highveld Grassland (6) or moister regions of the southwest (4).

Many *Onitis* species are assessed as Least Concern (LC) since they are mostly widespread in farmland and reserves (18) or are currently well protected in reserves along with elephants and/or zebra (5). However, a number (9) are assessed as Data Deficient (DD) since they are poorly known ecologically and have been recorded from few localities over large or very small areas. In some cases, species assessed as DD may be threatened.

In southern Africa:

Group III: Seven species; one savanna species widespread to E Africa, one savanna and Highveld Grassland species widespread into the SW Palaearctic region; five southern African species, either centred to the south (1), on Highveld grasslands (3) or in savanna and Highveld Grassland (1); mostly widespread in farmland.

Group VII: Five species in a cool-adapted species group; all restricted to southern Africa; four showing cool season activity, either southerly biased in winter rainfall (1) or mainly summer rainfall regions (2) or with relatively widespread range (1); one showing summer activity centred on Highveld Grassland; diurnal flight activity in two southernmost species.

Group IX: Two savanna species with widespread distributions to E or E and W Africa; at least one is a monogastric dung specialist on finer-grained soils in woodland.

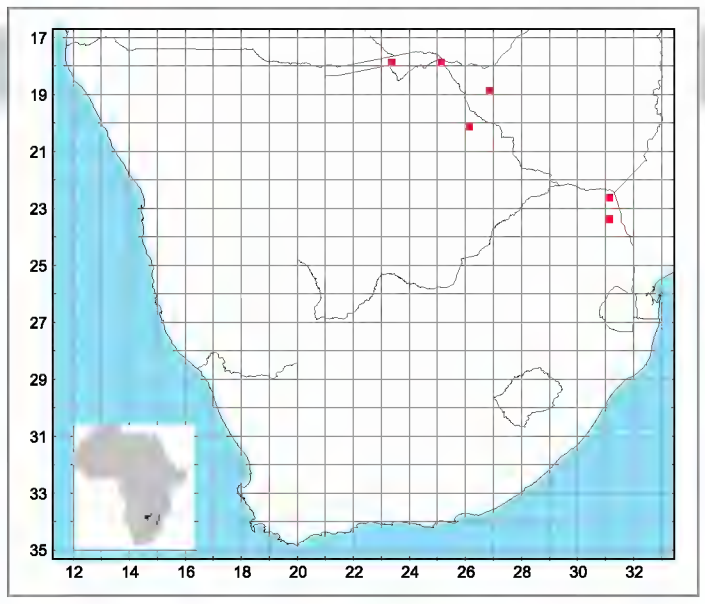
Group XI: Four southern African species centred on arid to dry savanna with a probable bias to association with dung of monogastric herbivores; bias in soil associations shown by at least two species. One further species possibly undescribed at present.

Group XII: One southern African, dry savanna species with probable specialist associations.

Group XVII: Four savanna species; three centred in southern Africa, one distributed to E Africa; at least three associated primarily with woody habitat.

Group XVIII: Five species, four centred in arid to mostly dry savanna, one on Highveld Grassland; all associated with dung of monogastric herbivores although two equally attracted to pads of ruminant herbivores; four species restricted to southern Africa, including a sand specialist, one finer-grained soil specialist distributed to E Africa.

Group XIX: Four savanna species with fragmented distributions centred on game reserves owing to association with dung of monogastric herbivores; possibly all associated with woody vegetation; two southern African sand specialists, two on finer-grained soils with distributions extending to E Africa.



Onitis aeruginosus

Klug, 1855

= *Onitis granulisetosus* Ferreira, 1976a

Global: LC (see IUCN Red List: *O. aeruginosus* – DD, *O. granulisetosus* – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. aeruginosus*: 'Sena' [Sena, Zambezi Valley, Mozambique]; *O. granulisetosus*: 'Rhodesia : nº 1310, Wankie N.P. (Nr. Sinamatella)' [Hwange National Park, Zimbabwe].

Taxonomy: Accepted Group XI species; limited sexual dimorphism (legs), prominence of characters varies with body size.

Distribution: Dry to moist lowland savanna on deep sands at NE edge of Kalahari plus Zambezi Valley, also inland sand pockets on Mozambique Coastal Plain: NE Namibia, N Botswana, N Zimbabwe, S Mozambique, NE South Africa.

Locality data (mean ± SD, range): Altitude: 701 ± 331, 114–1 106 m; annual rainfall: 586 ± 93, 418–681 mm; annual temperature (max. + min. /2): 23.0 ± 1.6, 21.1–26.7°C (N=10).

Habitat: No quantitative assessment; severely limited DBRU collection records on sand (1) or sandy loam (1) in open shrub/woodland (1).

Food types: On deep sand in Botswana: sampled only to dung of elephant (15) and pig (10), not dung of cattle (0), sheep (0) or carrion (chicken livers: 0); severely limited DBRU collection records on dung of elephant (1), cattle (1).

Temporal activity: Flight activity in darkness during summer rainy season (Dec. to Mar.).

Ecoregions Namibia, Botswana, Zimbabwe: Zambezian and Mopane Woodlands (AT0725), Zambezian Baikiaea Woodlands (AT0726), Kalahari Acacia-Baikiaea Woodlands (AT0709).

Bioregions South Africa: Mopane (SVmp) (Savanna Biome).

Assessment rationale: EOO = 134 325 km^2; AOO probably much smaller due to putative soil and dung type specialisation; thought to be a deep sand specialist in open woodland, but support currently severely limited; limited data suggest specialisation to dung of omnivores and large monogastric herbivores; assessed as Least Concern (LC) since most records are from protected areas.

Conservation measures: Assessment of conservation status would be improved by quantitative data on habitat associations and data to determine the importance to population density of large monogastric herbivores given the greater frequency of *O. aeruginosus* records in reserves; protected in Hwange, Chobe and Kruger national parks (Zimbabwe, Botswana, South Africa).

Onitis alexis

Klug, 1835

= *Onitis aygulus* Latreille, 1804
= *Onitis inuus* Klug, 1862
= *Onitis sphinx* Harold, 1871b
= *Onitis africanus* Gillet, 1909
= *Onitis africanus* var. *tuberculatus* Gillet, 1909

subsp. *septentrionalis* Balthasar, 1942

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. alexis*: *nom nov.* for *O. aygulus* Latreille (pre-occupied name): 'Depuis la Barbarie jusqu'au cap du Bonne-Espérance' [from North Africa almost to the Cape of Good Hope]; *O. inuus*: 'von Inhambane als früher von Tette und Sena' [Mozambique: Inhambane, Tete and Sena]; *O. sphinx*: 'Keren und Insaba' [Eritrea: Keren and Ansaba]; *O. africanus* plus var.: 'Koulikoro' [Mali]; subsp. *septentrionalis*: Not stated.

Taxonomy: Accepted Group III species; limited sexual dimorphism (legs), prominence of characters varies with body size.

Distribution: Arid to moist African savannas S of the Sahara: South Africa, Namibia, Botswana, Eswatini, Zimbabwe, Angola, Zambia, Mozambique, Tanzania, Kenya, Eritrea, Nigeria, Côte d'Ivoire, Mali; also reported from Cameroon, Niger, Ghana, Senegal, Mauritania; circum-Mediterranean populations of N Africa, Middle East and S Europe (Morocco to Syria, Greece to S Spain) separated as subsp. *septentrionalis* (range not shown).

Locality data (mean ± SD, range): Altitude: 981 ± 452, 0–2 199 m; annual rainfall: 600 ± 206, 71–1 659 mm; annual temperature (max. + min. /2): 19.3 ± 2.4, 11.2–25.2°C (N=574).

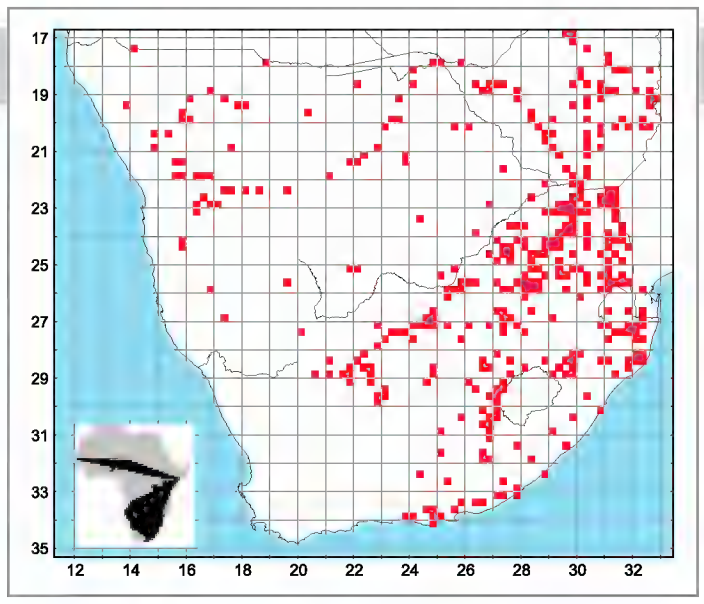
Habitat: In Gauteng bushveld: soil generalist with a bias to more open vegetation, deep sand (56), sandy clay loam (84), grassland (79), open woodland (35), shaded thickets (26); largely supported by DBRU collection records: clay (13), sandy clay loam (101), sandy loam (112), sand (100) in crop fields (11), pasture/grassland (154), open shrub/woodland (128), forest/thickets (7).

Food types: No quantitative assessment; DBRU collection records on cattle (370) and horse (6) dung in farmland, also in reserves on dung of buffalo (13), elephant (17) and zebra (2), with single records on hooked-lipped (black) rhinoceros and hippopotamus dung.

Temporal activity: Diel flight activity in darkness (crepuscular: dusk) (Caveney et al. 1989), primarily in the summer rainy season (Sept. to June); in Gauteng bushveld: peak activity in the early (Oct., Nov.) and late summer (Jan., Feb.); also tolerant of drier conditions (Sept.; May, June); bias to colonisation of fresh dung (0–2 days old, 50%; 2–4 days, 35%; N=175); attracted to light.

Ecoregions Namibia, Botswana, Zimbabwe, Mozambique: Arid: Kalahari Xeric Savanna (AT1309), Namibian Savanna Woodlands (AT1316); Mesic: Southern African Bushveld (AT0717), Zambezian and Mopane Woodlands (AT0725), Angolan Mopane Woodlands (AT0702), Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian Baikiaea Woodlands (AT0726), Southern Miombo Woodlands (AT0719), Maputaland Coastal Forest Mosaic (AT0119).

Bioregions South Africa: East Kalahari Bushveld (SVk), Central Bushveld (SVcb), Lowland (SVl), Mopane (SVmp), Sub-Escarpment



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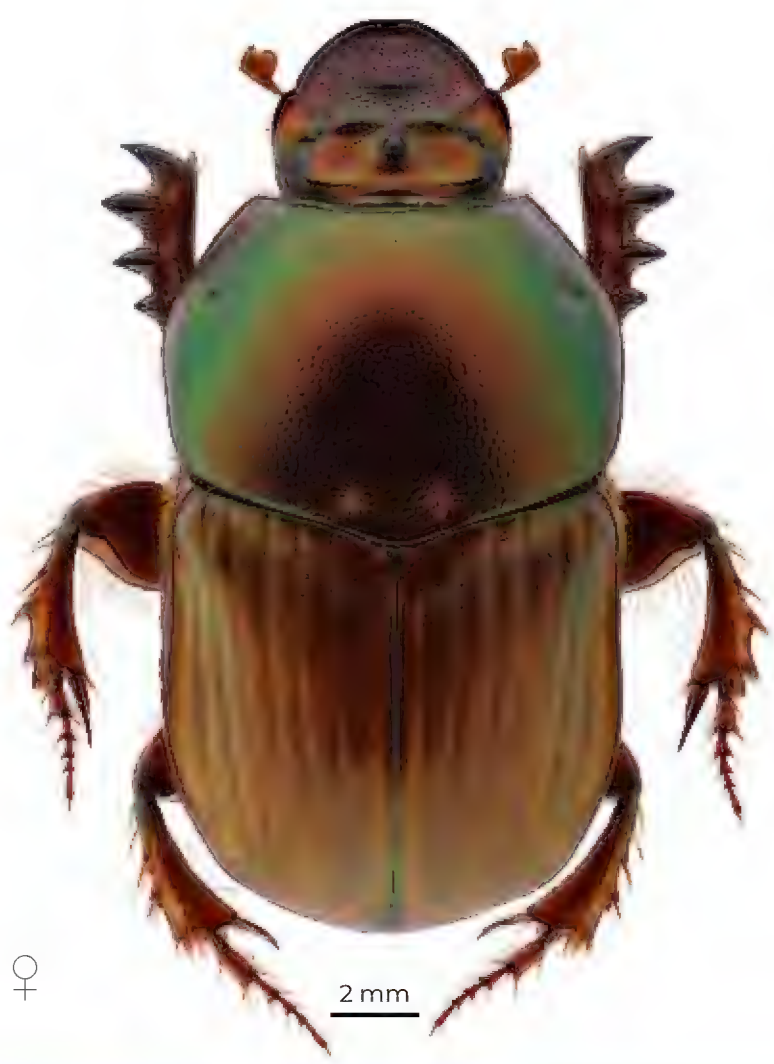

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Onitis alexis (continued)

Savanna (SVs) (Savanna Biome); Dry Highveld Grassland (Gh), drier units of Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs) (Grassland Biome); Albany Thicket Biome (AT); marginal in six other bioregions/biomes.

Assessment rationale: EOO = 9 990 325 km² (S of Sahara, gross estimate); exceptionally widespread soil generalist in more open vegetation of both reserves and farmland where it readily colonises the dung of both indigenous mammals and domestic livestock; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on food associations; occurs in many reserves including Kruger National Park (South Africa), Gorongosa National Park (Mozambique), Serengeti National Park (Tanzania), Yankari Game Reserve (Nigeria).

Onitis aygulus

(Fabricius, 1781)

= *Scarabaeus inuus* Herbst, 1789

Global: LC
Endemic: RSA, Botswana, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Scarabaeus aygulus*: 'India' [cited type locality is an error]; *S. inuus*: Not stated.

Taxonomy: Accepted Group III species; limited sexual dimorphism (legs), prominence of characters varies with body size.

Distribution: Dry climate bordering arid areas in winter, bimodal and late summer rainfall regions of SW Africa; mainly S coastal and central South Africa but also S margins of Namibia and Botswana with scattered records in arid regions.

Locality data (mean ± SD, range): Altitude: 971 ± 508, 0–2 410 m; annual rainfall: 356 ± 133, 67–741 mm; annual temperature (max. + min. /2): 16.9 ± 2.2, 8.9–21.2°C (N=157).

Habitat: No quantitative assessment; DBRU collection records from sand (25), sandy loam (32), sandy clay loam (22) and clay (3) on pasture or grassland (28), scrub/shrubland (26), open woodland (6); also in fallow crop fields (6).

Food types: No quantitative assessment; DBRU collection records mostly from cattle dung (88) with one from buffalo dung.

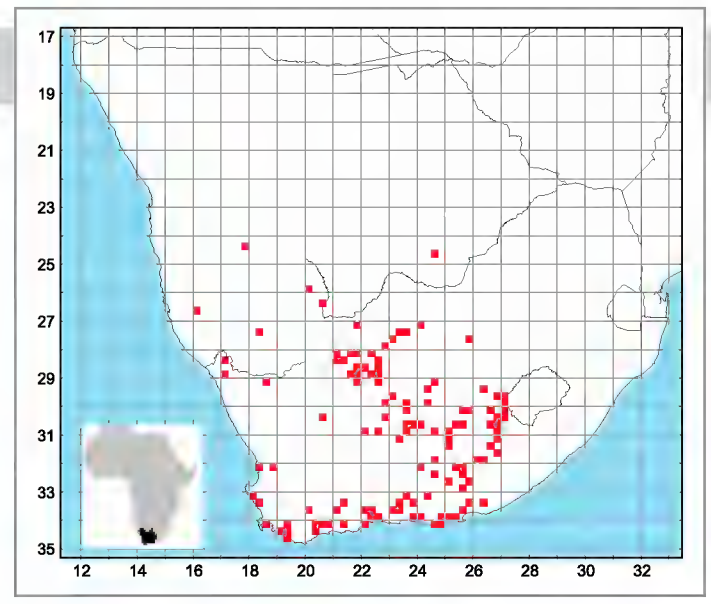
Temporal activity: Diel flight activity in darkness (crepuscular: dusk/dawn and nocturnal) (Caveney et al. 1989) in the warmer summer in all regions (Oct. to May), irrespective of rainfall periodicity.

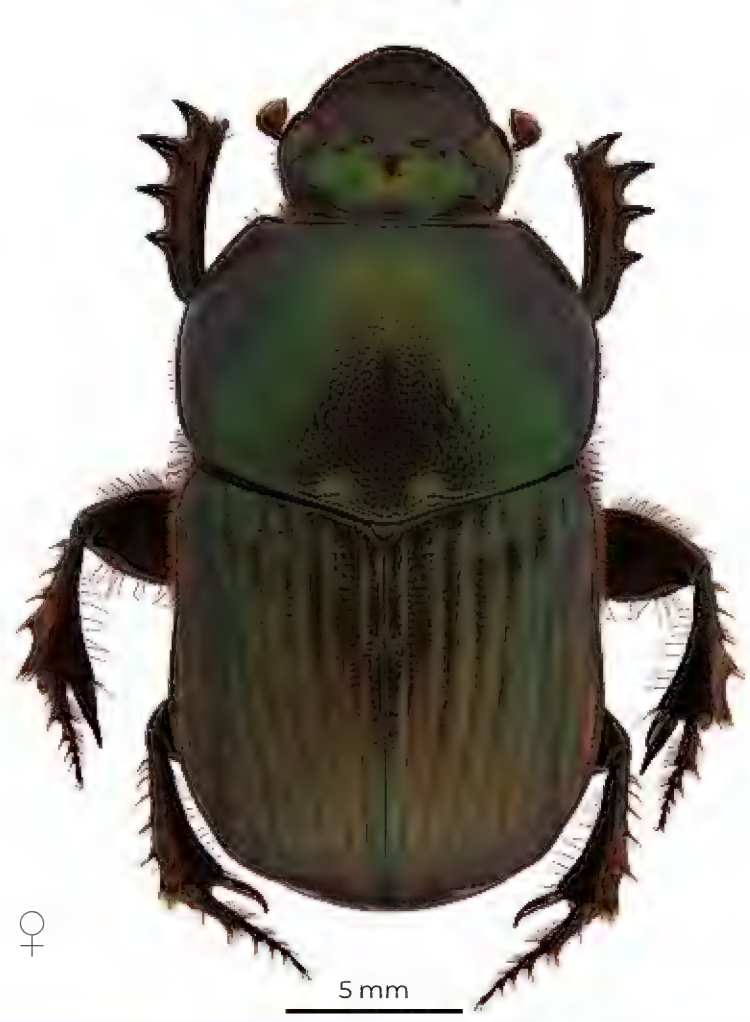
Ecoregions Namibia, Botswana: S Kalahari Xeric Savanna (AT1309), Succulent Karoo (AT1322).

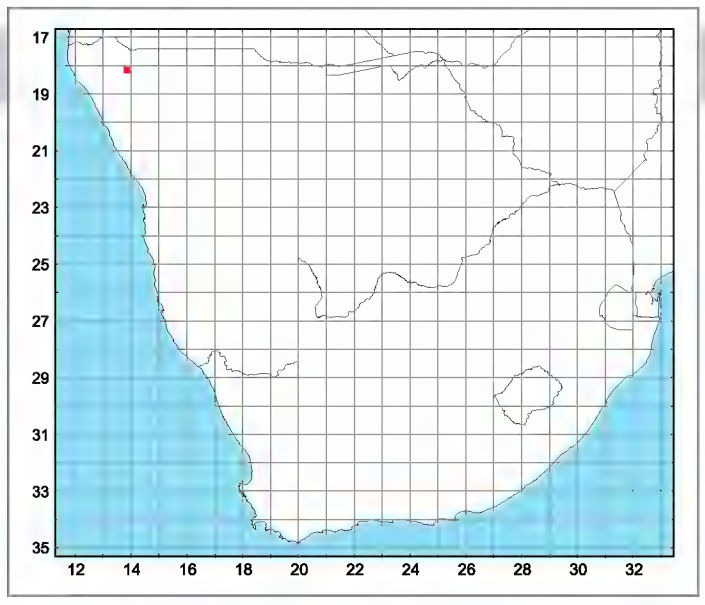
Bioregions South Africa: In the NW: bioregions along the boundaries of the Savanna (Eastern Kalahari Bushveld (SVk)), Grassland (S Dry Highveld Grassland (Gd)) and Nama Karoo (Upper Karoo (NKu)) biomes; in the S: Albany Thicket (AT) and Fynbos (F) biomes.

Assessment rationale: EOO = 756 700 km²; widespread on different soil types with vegetation associations reflecting its range across both dry grassland and shrubland-dominated bioregions; DBRU collection records in Fynbos Biome (34°S 19–25°E) are all in pastures or crop fields and suggest possible past range expansion in response to transformation of natural shrubland vegetation; along S coast variable transformation (AT, F: 4–80%); NW part of range used primarily for grazing of farm livestock and little transformed (SV, NK, G: 0–4%); assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; protected in Addo Elephant National Park.







Onitis bilobatus

Ferreira, 1976a

No synonyms

Global: DD
Endemic: Namibia

| J | A | S | O | N | D | J | F | M | A | M | J |

Type locality: 'South West Africa : Opuwo 18° 03' S, 13° 50' E, Kaokoland' [N Namibia].
Taxonomy: Accepted Group XVIII species known only by the male holotype; should be compared with Group XVIII relative, *O. mniszechi* van Lansberge, 1886, described from Damaraland, but appears to differ.
Distribution: Type locality in dry N Namibian savanna.
Locality data: Altitude: 1264 m; annual rainfall: 367 mm; annual temperature (max. + min. /2): 17.0°C (N=1).
Habitat: No quantitative assessment; unknown.
Food types: No quantitative assessment; association unknown, but relatives in Group XVIII have been recorded partly or entirely from dung of monogastric herbivores.
Temporal activity: Probable flight activity in darkness in the late summer rainy season.
Ecoregions Namibia: N Namibian Savanna Woodlands (AT1316).
Assessment rationale: EOO unknown; known by a single specimen from a dry savanna region; currently assessed as Data Deficient (DD).
Conservation measures: A quantitative survey at the E edge of the arid Kaokoveld and surrounding regions is required to determine the EOO, AOO, and ecological associations and how these differ from *O. mniszechi*; not currently known to occur in any protected area.

Onitis caffer

Boheman, 1857

= *Onitis nicanor* LeConte, 1861

Global: LC (see IUCN Red List – LC)
Endemic: RSA, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. caffer*: 'Caffraria tota' [inexact, all of SE South Africa]; *O. nicanor*: 'Southern States' [described in error as showing very rare occurrence in southern USA].

Taxonomy: Accepted Group VII species; limited sexual dimorphism (legs), prominence of characters varies with body size; very close relative of *O. perpunctatus* Balthasar, 1963, but differs in seasonality; isolated highland population in central Namibia needs to be compared with South African individuals when more reference material is available.

Distribution: Moister regions in E half of South Africa as well as S and SW coastal regions; outlier population in central uplands, Namibia; also cited from Lesotho; Mozambique citation requires validation, possibly confused with *O. autumnalis* Davis, 1986.

Locality data (mean ± SD, range): Altitude: 990 ± 277, 0–2 274 m; annual rainfall: 585 ± 182, 120–1 047 mm; annual temperature (max. + min. /2): 17.0 ± 2.0, 10.6–22.6°C (N=275).

Habitat: No adequate quantitative assessment; at warmer N limit of range in Gauteng bushveld: sampled on both deep sand (35) and sandy clay loam (18); on sand: bias to shaded thicket (29) compared to open woodland (5) and grassland (1), but, on sandy clay loam: bias to grassland (12) compared to open woodland (4) and shaded ticket (2); DBRU collection records biased to finer-grained soils: sand (31), sandy loam (60), sandy clay loam (71), clay (5), with a bias to open vegetation: grassland/pasture (96), scrub/shrubland (17), open woodland (17), forest (1), also fallow or harvested crop fields (15).

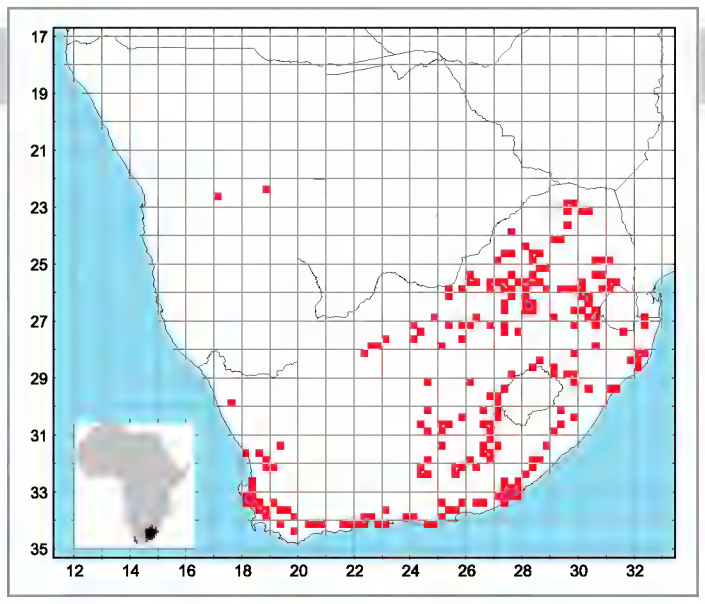
Food types: No quantitative assessment; DBRU collection records primarily from cattle dung (210), but also dung of buffalo (3), horse (1), elephant (1), rhinoceros (1) and human/cattle dung mix (2).

Temporal activity: Diel flight activity in darkness (crepuscular: dusk) (Caveney et al. 1989); records from every month of the year, but primarily active during cooler months in autumn, winter and spring; seasonal bias varies regionally; on Darling Hills in cooler Western Cape, winter rainfall region: sampled Mar. to Sept.; on warmer Gauteng bushveld: sampled at cooler end of summer rainy season and beginning of dry season (Apr. to June); only 6% (14/228) of DBRU collection records during Nov. to Jan.

Ecoregions Namibia: NW Kalahari Xeric Savanna (AT1309).

Bioregions South Africa: East Kalahari Bushveld (SVk), Central Bushveld (SVcb), margins of Lowveld (SVl) (Savanna Biome); Dry Highveld Grassland (Gh), Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs) (Grassland Biome); moister E Upper Nama Karoo (NKu) (Nama Karoo Biome); Albany Thicket Biome (AT); Fynbos Biome in areas cleared of natural shrubland and replaced with pasture or crop fields; marginal in Succulent Karoo Biome (SK).

Assessment rationale: EOO = 576 190 km^2; widespread across natural grassland and transformed pasture vegetation, primarily in South African farmland; records from fallow and harvested crop fields suggest tolerance of extreme habitat transformation; presence in transformed



Onitis caffer (continued)

pastures and arable lands along S and SW South Africa coast may or may not represent range expansion in response to clearance of natural shrubland; owing to known associations and tolerance of habitat modification, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by further quantitative ecological data from different climatic regions of South Africa and central Namibia; protected in several national parks including Bontebok and Addo Elephant.

Onitis confusus

Boheman, 1860

= *Scarabaeus inuus* Fabricius, 1781

Global: LC
Endemic: RSA, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. confusus*: 'juxta fluvium Svakop' [near Swakop River, Namibia]; *S. inuus*: 'Sierra Leon' [cited synonymy undoubtedly an error if Sierra Leone type locality is correct].

Taxonomy: Accepted Group VII species; limited sexual dimorphism (legs), prominence of characters varies with body size.

Distribution: SW African endemic; primarily South Africa; Namibian records represented by only the type locality; citations from tropical Africa are considered as errors (Sierra Leone, Kenya, Tanzania, Democratic Republic of the Congo (DRC), Malawi, Zimbabwe, Mozambique).

Locality data (mean ± SD, range): Altitude: 603 ± 567, 0–1 536 m; annual rainfall: 298 ± 126, 9–666 mm; annual temperature (max. + min. /2): 16.6 ± 1.6, 14.0–20.3°C (N=34).

Habitat: No quantitative assessment; DBRU collection records dominated by sand (18), mainly from SW coast, but also sandy clay loam (3), sandy loam (3); primarily from low profile vegetation, either natural scrub (6), or disturbed by clearance of fynbos shrubs = pasture/grassland (4), cleared patches (7), fallow crop fields (2); few in shrub/woodland (3).

Food types: No quantitative assessment; DBRU collection records from cattle (16), horse (5) and donkey (1) dung.

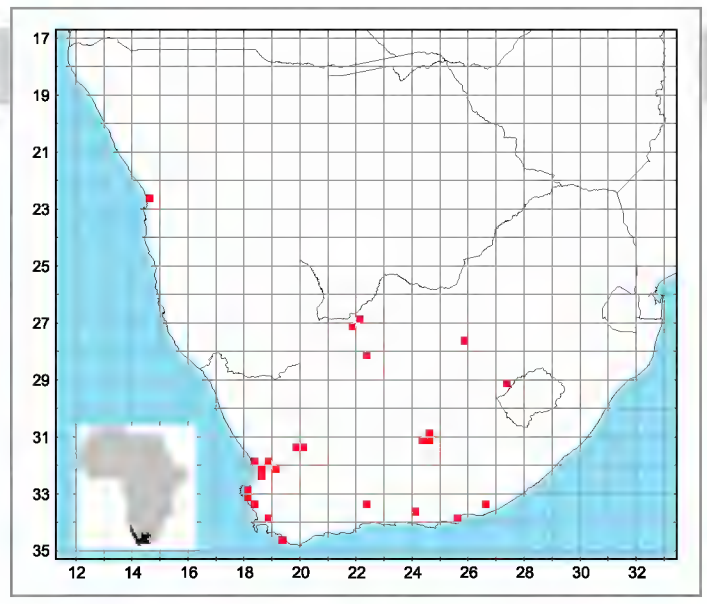
Temporal activity: Flight activity in darkness during autumn, winter and spring (Mar. to Oct.), which is consistent with the seasonal rainfall across the depicted range in the winter, bimodal and late summer rainfall regions of southern Africa.

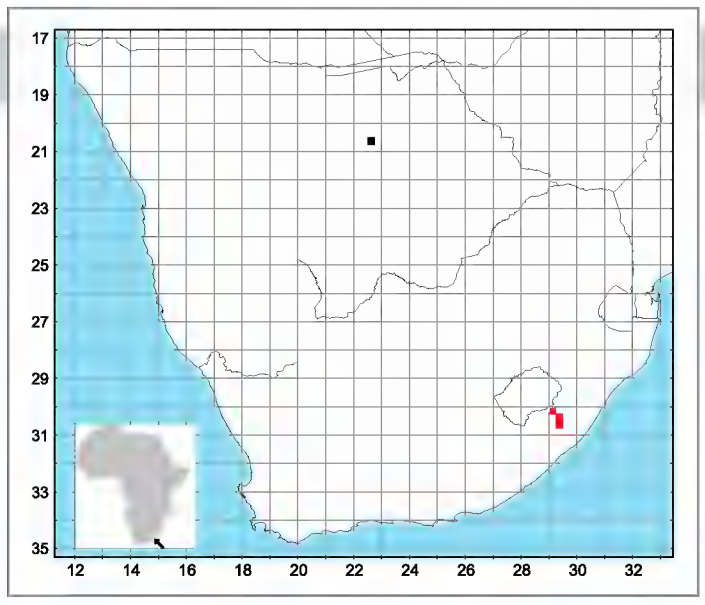
Ecoregions Namibia: Cited type locality in the Namib Desert (AT1315).

Bioregions South Africa: Records scattered in various bioregions; SW of Savanna (SV) and Grassland (G) biomes; also Nama Karoo (NK), Albany Thicket (AT), Fynbos (F) and S of Succulent Karoo (SK) biomes.

Assessment rationale: EOO = 529 675 km^2; as many SW records are from disturbed habitats, current range may or may not represent that occupied in the past; data inadequate to determine natural associations, but probably a soil generalist in low profile vegetation; widespread and tolerant of disturbance.

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations and a survey to better determine the EOO and AOO; possibly protected in West Coast National Park, but most past records from sparse grassland are in areas of the park now restored to shrubland.





Onitis cribratus

van Lansberge, 1875b

No synonyms

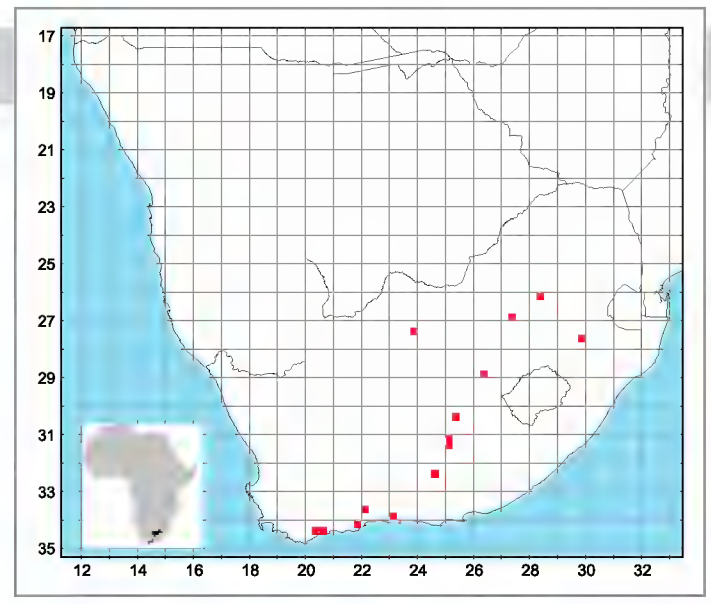
Global: DD
Endemic: RSA, Botswana (?two different species)

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Caffrerie intérieure (N'Gami)' [Lake Ngami, N Botswana].
Taxonomy: Accepted Group III species, but type locality either incorrect or species cited as *O. cribratus* by Ferreira (1978) differs from that described from two individuals (♂ + ♀) by van Lansberge (1875b), who cites it as being very rare and larger than *O. pecuarius* van Lansberge, 1875b; limited sexual dimorphism (head, legs).
Distribution: Species cited as *O. cribratus* by Ferreira (1978) (see photograph) is hardly larger than *O. pecuarius* and occupies a small, wet, highland grassland range restricted to South Africa, E of Lesotho, where it is uncommon (red squares); Lake Ngami type locality (black square) is climatically quite different.
Locality data (mean ± SD, range): Highland data only: average altitude: 1 430 ± 131, 1 305–1 582 m; average annual rainfall: 762 ± 16, 744–775 mm; average annual temperature (max. + min. /2): 14.6 ± 0.4, 14.3–15.0°C (N=3).
Habitat: No quantitative assessment; limited DBRU collection records on sandy loam (1), sandy clay loam (1) in grassland (1), pasture (1).
Food types: No quantitative assessment; limited DBRU collection records on dung of cattle (2).
Temporal activity: Flight activity in darkness during the summer rainy season (Dec. to Feb.).
Ecoregions Botswana: Type locality cited as Lake Ngami: Kalahari Acacia-Baikiaea Woodlands (AT0709).
Bioregions South Africa: Central Sub-Escarpment grassland (Gs) (Grassland Biome).
Assessment rationale: EOO = 265 km^2 (grossly underestimated); highland individuals likely represent an undescribed species confused with *O. cribratus*, which is known from only two specimens at the type locality; the highland species is uncommonly recorded on cattle dung in grassland/pasture on farmland; although habitat transformation or loss of particular dung types from ranges are possible influences on rarity of both species, these remain unknown; both assessed as DD.
Conservation measures: A comparison between South African highland individuals and the type specimens of *O. cribratus* is required to resolve probable taxonomic confusion; depending on the results, a quantitative survey of the type locality and the highlands E of Lesotho needs to be conducted to determine EOO, AOO and ecological associations of what is likely two different species; neither is currently known to occur in protected areas.

Onitis curvipes

van Lansberge, 1875b



No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Cap de Bonne-Espérance' [Cape of Good Hope, South Africa].

Taxonomy: Accepted Group XVIII species; limited sexual dimorphism (head, legs), prominence of characters varies with body size.

Distribution: Highveld of South Africa; further records from the S coast, one from pasture after clearance of natural shrubland, others without citations of vegetation type; records from Angola, Zimbabwe, Mozambique, Botswana, Namibia, probably errors.

Locality data (mean ± SD, range): Altitude: 914 ± 621, 33–1 632 m; annual rainfall: 458 ± 156, 256–787 mm; annual temperature (max. + min. /2): 16.7 ± 1.3, 13.4–18.8°C (N=14).

Habitat: No quantitative assessment; single DBRU collection records from clay, sandy clay loam, sandy loam, sand on limestone, natural grassland and pasture.

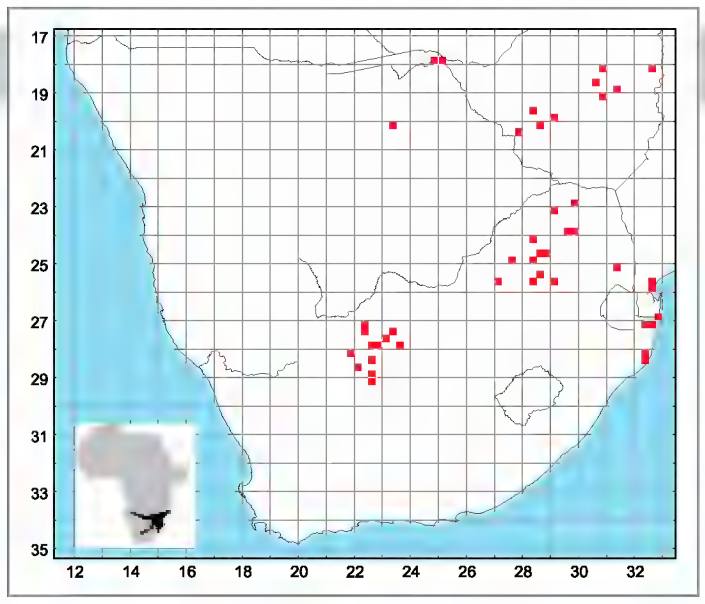
Food types: No quantitative assessment; DBRU collection records from horse (3), zebra (1), donkey (1) and cattle (2) dung.

Temporal activity: Flight activity in darkness during the summer rainy season (Oct. to Apr.).

Bioregions South Africa: In NW: Dry Highveld Grassland (Gd), Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs) (Grassland Biome), E Upper Karoo (NKu) (Nama Karoo Biome), Eastern Kalahari Bushveld (SVk) (Savanna Biome); In SW: Little Karoo (NKl) (Nama Karoo Biome), Shale Renosterveld (FRs), Sandstone Fynbos (FFs) (Fynbos Biome).

Assessment rationale: EOO = 150 365 km²; cited as very rare in original description, possibly because of association with the dung of monogastric herbivores at a time when population density of such indigenous mammals was already depleted across its range; because of the wide range, would not qualify for an IUCN threat category; poorly known and assessed as Data Deficient (DD).

Conservation measures: Quantitative data on ecological associations is required before an assessment may be made of conservation status, particularly, tests for specialisation to monogastric herbivore dung, which may be the reason for continuing low population density across its grassland/pasture range; not currently known from any protected area.



Onitis deceptor

Péringuey, 1901

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'Southern Rhodesia (Enkeldorn, Buluwayo)' [Zimbabwe: Chivhu, Bulawayo].

Taxonomy: Accepted Group XVIII species; limited sexual dimorphism (head, legs), prominence of characters varies with body size.

Distribution: Dry to moist savannas of southern and southern central Africa: South Africa, Botswana, Zimbabwe, Mozambique, Angola, Malawi; patchy occurrence in Kalahari outliers and other pockets of deep sands, including SE coast; also reported from Democratic Republic of the Congo (DRC), Tanzania, but requires validation.

Locality data (mean ± SD, range): Altitude: 961 ± 510, 0–1 698 m; annual rainfall: 625 ± 219, 235–1 220 mm; annual temperature (max. + min. /2): 19.9 ± 1.9, 16.3–23.4°C (N=62).

Habitat: Extreme deep sand specialist; in Gauteng bushveld and Bushlands Halt: respectively, deep sand (238, 230), sandy clay loam/clay loam (0, 4); in Gauteng bushveld: bias to woody vegetation, grassland (37), open woodland (133), shaded thickets (68); at Bushlands Halt: bias to open rather than shaded vegetation, grassland (189), dense shrubland (45).

Food types: No adequate quantitative assessment; in Botswana: sampled from pig (1), elephant (3), cattle (1) and sheep (2) dung; DBRU collection records entirely from cattle dung (21).

Temporal activity: Flight activity in darkness during the summer rainy season (Nov. to Apr.); strong bias to colonisation of fresh dung (0–1 days old, 71%; 1–2 days, 21%; N=34).

Ecoregions Botswana, Zimbabwe, Mozambique: Deep sand: Zambezian and Mopane Woodlands (AT0725), Southern African Bushveld (AT0717), Southern Miombo Woodlands (AT0719), Maputaland Coastal Forest Mosaic (AT0119).

Bioregions South Africa: Deep sand: W East Kalahari Bushveld (SVk), Central Bushveld (SVcb) (Savanna Biome), N Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 1 264 130 km^2 (probably underestimated); widespread EOO, but smaller, patchy AOO in a number of discrete population centres owing to soil type specialisation; readily attracted to cattle dung in farmland; population density could be markedly reduced by clearance of woodland on sand in SVcb, but also fairly abundant in deep sand grassland in CB; transformation: 0–2% (W SVk), 2–49% (SVcb); assessed as Least Concern (LC).

Conservation measures: Conflicting habitat results suggest assessment of conservation would be improved by further quantitative data on vegetation associations and data on dung type associations; protected in Chobe National Park (Botswana), Tembe Elephant Park (South Africa).

Onitis fabricii

Roth, 1851

= *Onitis perplexus* Boheman, 1857
= *Onitis vethi* van Lansberge, 1886
= *Onitis obscuratus* Fairmaire, 1893

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. fabricii*: 'Abyssinien' [Ethiopia]; *O. perplexus*: 'Caffraria tota' [all SE South Africa]; *O. vethi*: 'Humpata' [Angola]; *O. obscuratus*: 'du Choa…sans indication de la localité précise' [no exact locality, Choa, Ethiopia].

Taxonomy: Accepted Group IX species; limited sexual dimorphism (legs), prominence of characters varies with body size; unless Boheman used Caffraria in a geographically wide sense, type locality of synonym, *O. perplexus*, lies outside of known modern range of *O. fabricii*.

Distribution: Dry to moist savanna from southern to NE Africa: N South Africa, Zimbabwe, Mozambique, Angola, Kenya, Ethiopia; also reported from Democratic Republic of the Congo (DRC).

Locality data (mean ± SD, range): Altitude: 999 ± 441, 59–1 698 m; annual rainfall: 713 ± 174, 562–1 180 mm; annual temperature (max. + min. /2): 20.1 ± 2.1, 16.0–25.2°C (N=22).

Habitat: No quantitative assessment; DBRU collection records on finer-grained soils: clay (1), sandy clay loam (1), sandy loam (3), in both pasture (4) and open woodland (2).

Food types: No quantitative assessment; DBRU collection records on both cattle (6) and elephant (2) dung.

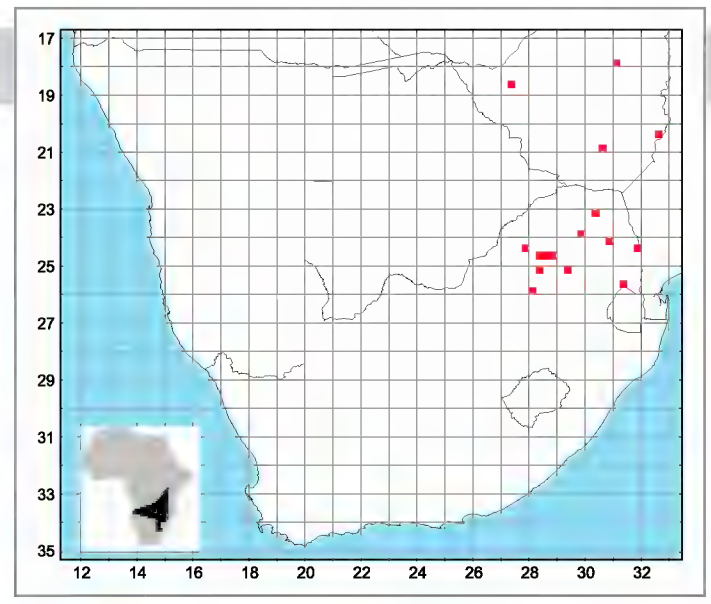
Temporal activity: Flight activity in darkness during the summer rainy season (Nov. to Apr.).

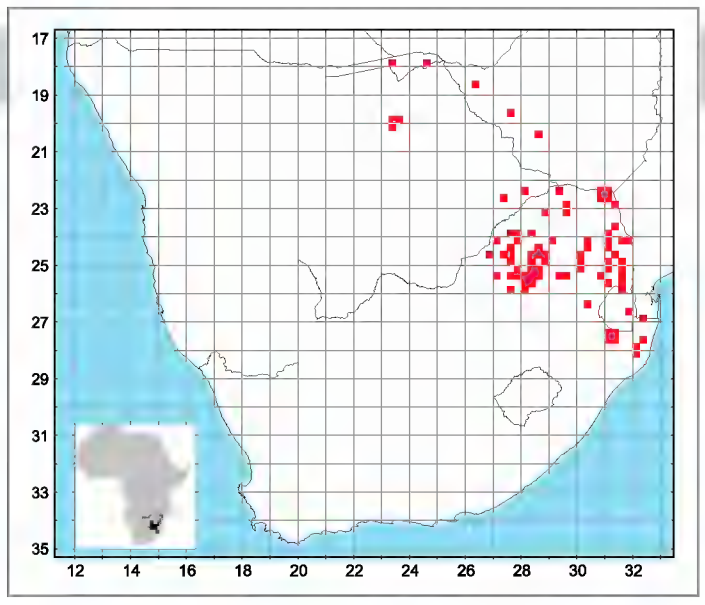
Ecoregions Zimbabwe: Zambezian Baikiaea Woodlands (AT0726), Zambezian and Mopane Woodlands (AT0725), Southern Miombo Woodlands (AT0719).

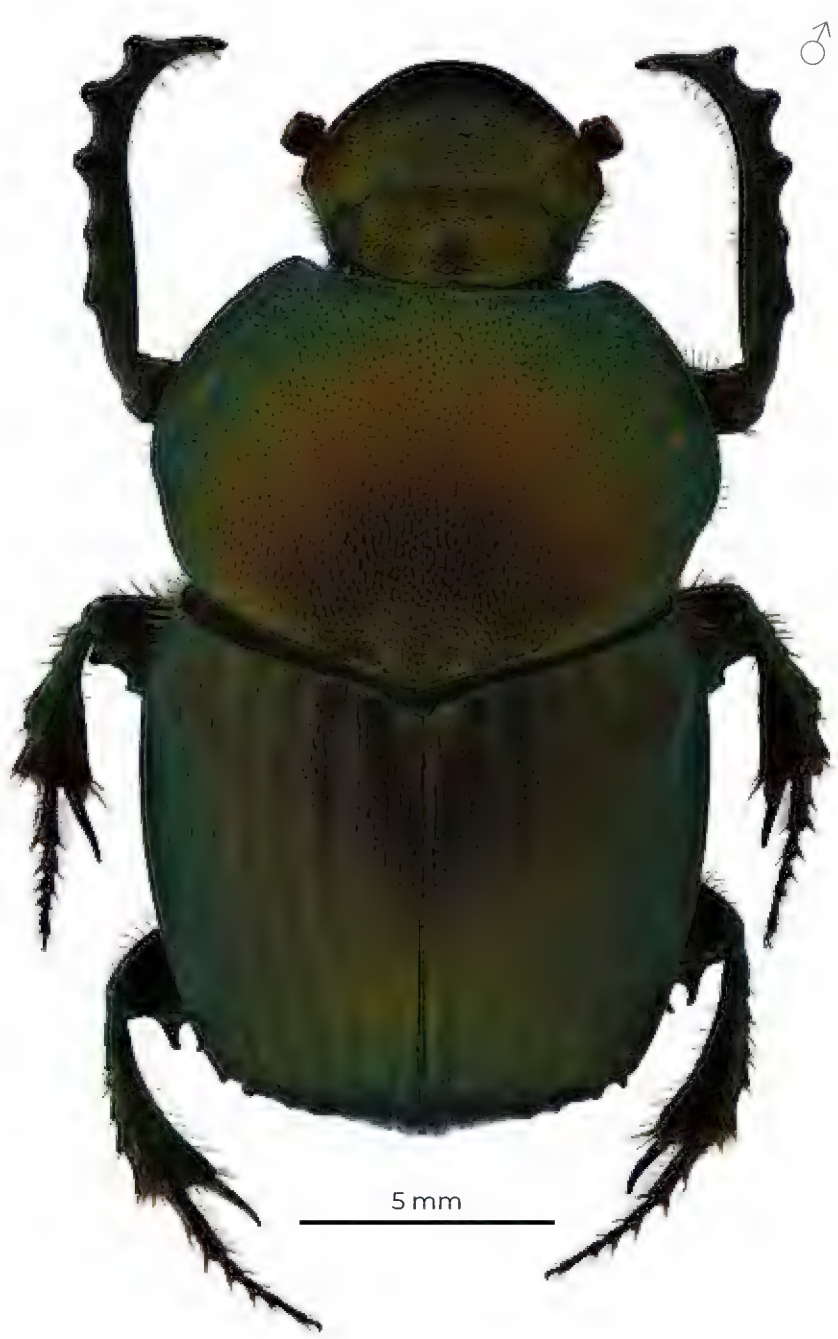
Bioregions South Africa: Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 2 595 525 km² (underestimated); ecological data insufficient to assess conservation status of this uncommon species; widespread occurrence suggests that it is not currently threatened despite apparently low population density, assessed as Least Concern (LC) rather than Data Deficient (DD).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; protected in Kruger (South Africa), Bicuar (Angola), Gorongosa (Mozambique) national parks.







Onitis fulgidus

Klug, 1855

= *Onitis klugii* Harold, 1859 *nom nov.*
= *Onitis cupreus* Castelnau, 1840, *sensu* Harold, 1871b (error)
= *Onitis aerarius* Harold, 1878, *sensu* Péringuey, 1901 (?*pars*)

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *Onitis fulgidus*: 'Sena und Tette' [central Mozambique: Sena and Tete]; *O. klugii* is the unrecognised *nom nov.* for *O. fulgidus* Klug, 1855; *O. cupreus sensu* Harold: 'Keren' [Eritrea – synonymy undoubtedly erroneous]; *O. aerarius sensu* Péringuey: 'Southern Rhodesia (Victoria Falls; Salisbury, Mazoe, Buluwayo)' [Zimbabwe: Victoria Falls; Harare, Mazoe, Bulawayo]. Occurs also in Nyassaland and the Galla country' [cited range in Zimbabwe, Malawi and Ethiopia suggests confusion between several species, one of which may be *O. fulgidus* Klug, 1855].

Taxonomy: Accepted Group XVII species, but name pre-occupied by *O. fulgidus* Castelnau, 1840, from Senegal, which is most unlikely to be the same species unless the type locality is an error; validation of nomenclature required; limited sexual dimorphism (legs), prominence of characters varies with body size.

Distribution: Owing to confusion between species, not possible to determine true range, but probably restricted to low-altitude, wooded savanna of SE southern Africa; N South Africa, N Botswana, NE Namibia, Zimbabwe to no further N than hot dry climates of the Zambezi Valley in S Zambia, S Malawi and central Mozambique; reports from Ethiopia, Kenya, Tanzania and Angola are errors.

Locality data (mean ± SD, range): Altitude: 832 ± 401, 52–1 529 m; annual rainfall: 633 ± 124, 286–1 145 mm; annual temperature (max. + min. /2): 20.4 ± 2.0, 15.4–25.9°C (N=112).

Habitat: Strong bias to finer-grained soils in both Gauteng bushveld and uMkhuze Game Reserve: sandy clay loam (80), deep sand (1) (Gauteng), clay (2.8), sandy clay loam (21.5), deep sand (5.7) (uMkhuze); in Gauteng bushveld: strong bias to shady woodland, thickets (46), open woodland (28), grassland (7); all DBRU collection records from shrub/woodland (10) on sand (5), sandy loam (5) or clay (1).

Food types: Limited data at Phalaborwa shows clear dung type bias: pig (12), elephant (6), cattle (2); DBRU collection records from various dung types: cattle (11), elephant (5), single records from wildebeest, hooked-lipped (black) rhinoceros and horse dung.

Temporal activity: Diel flight activity in darkness (crepuscular: dusk) (Caveney et al. 1989) in the summer rainy season (Nov. to Apr.); in Gauteng bushveld: seasonal peaks in Nov. to Dec. and Feb.; attracted to light.

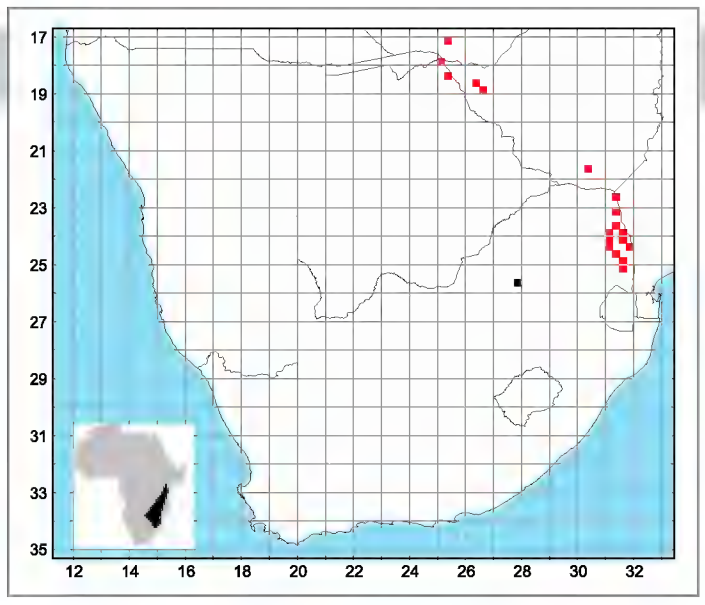
Ecoregions Botswana, Zimbabwe: Southern African Bushveld (AT0717), Zambezian and Mopane Woodlands (AT0725); marginal occurrence in two adjoining ecoregions.

Bioregions South Africa: Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome); marginal occurrence in two adjoining bioregions.

Assessment rationale: EOO = *circa* 366 000 km^2; widespread, but AOO smaller due to strong association with finer-grained soils in woodland whose clearance would represent a threat to population density of this species; transformation is 0–58% (SVl), 2–49% (SVcb); readily

colonises cattle dung in farm rangeland despite an apparent bias to other dung types; assessed as Least Concern (LC).

Conservation measures: Problems with nomenclature need to be resolved. Conservation status would be dependent on preservation of dense woody vegetation on finer-grained soils in SVcb and SVl; also useful to test possible effects of reduced dung type diversity on population density in farmland; protected in Kruger National Park, Ithala Game Reserve, Leeuwfontein and Tswaing nature reserves (South Africa).



Onitis inversidens

van Lansberge, 1875b

= *Onitis inversus* van Lansberge, 1875b
= *Onitis aeruscator* Gillet, 1918

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. inversidens*: 'Afrique australe' [southern Africa] *nom nov*. for *O. inversus* van Lansberge, a pre-occupied name; *O. aeruscator*: 'Abyssinie' [Ethiopia].

Taxonomy: Accepted Group XIX species; limited sexual dimorphism (legs), prominence of characters varies with body size.

Distribution: Patchy distribution in hot, mostly dry, savanna regions from SE to NE Africa according to patterns of range contraction by large monogastric herbivores to whose dung types *O. inversidens* is specialised; Brits locality (black square) possibly represents relict population, but occurrence needs confirmation; NE South Africa, NE Botswana, Zimbabwe, Mozambique, Tanzania, Kenya, Ethiopia; also cited from Malawi.

Locality data (mean ± SD, range): Average altitude: 545 ± 323, 59–1 131 m; average annual rainfall: 608 ± 143, 387–1 136 mm; average annual temperature (max. + min. /2): 22.4 ± 1.2, 19.2–25.2°C (N=24).

Habitat: No quantitative assessment; limited DBRU collection records from sand (1), sandy loam (3), sandy clay loam (1) in open woodland (5), dry forest (1).

Food types: No quantitative assessment; at Phalaborwa: limited quantitative data on dung of elephant (3), pig (1); DBRU collection records entirely from coarse-fibred dung of large monogastric herbivores: elephant (12), hooked-lipped (black) rhinoceros (1).

Temporal activity: Flight activity in darkness during the summer rainy season (Nov. to Mar.); attracted to light.

Ecoregions Botswana, Zimbabwe: Red squares: Zambezian and Mopane Woodlands (AT0725).

Bioregions South Africa: Red squares: Mopane (SVmp), N Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 1 704 640 km² (underestimated); AOO much smaller and patchy according to range contraction of monogastric herbivores; all southern African, DBRU records (15) are from game reserves or protected areas containing elephants; in addition to dung type specialisation, there is possible further reduction in AOO due to bias to finer-grained soils in wooded areas, but this requires testing; however, present in various protected reserves over a very wide range; therefore, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on habitat associations; observational data suggests continuing protection of large monogastric herbivores would be essential for conservation of this species; protected in various national parks: Kruger (South Africa), Hwange (Zimbabwe), Manyara (Tanzania), Tsavo East, Tsavo West (Kenya).

Onitis licitus

Péringuey, 1901

No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Cape Colony (Burghersdorp)' [Burgersdorp, Eastern Cape, South Africa].

Taxonomy: Accepted Group VII species; limited sexual dimorphism (legs), prominence of characters varies with body size.

Distribution: Known from few localities on the S Highveld, Eastern Cape, South Africa.

Locality data (mean ± SD, range): Altitude: 1 619 ± 258, 1 436–1801 m; annual rainfall: 528 ± 75, 475–581 mm; annual temperature (max. + min. /2): 13.7 ± 1.6, 12.6–14.8°C (N=2).

Habitat: One DBRU collection record from sandy clay loam in grassland.

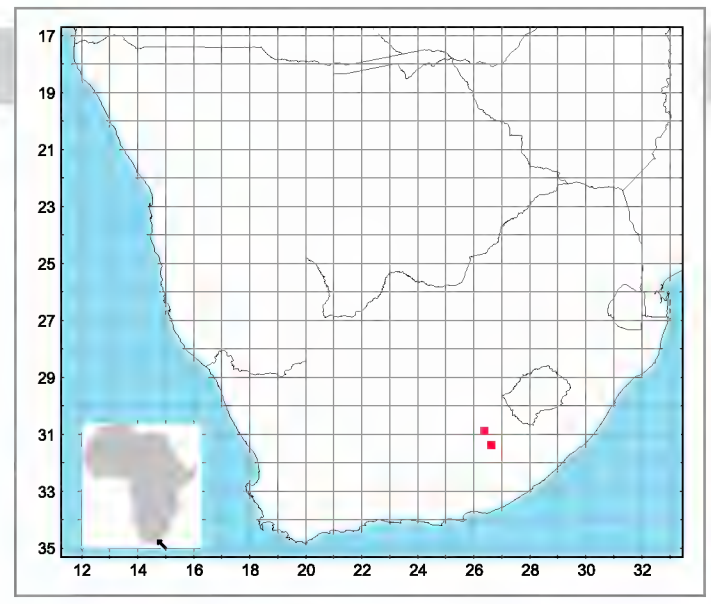
Food types: One DBRU collection record from cattle dung.

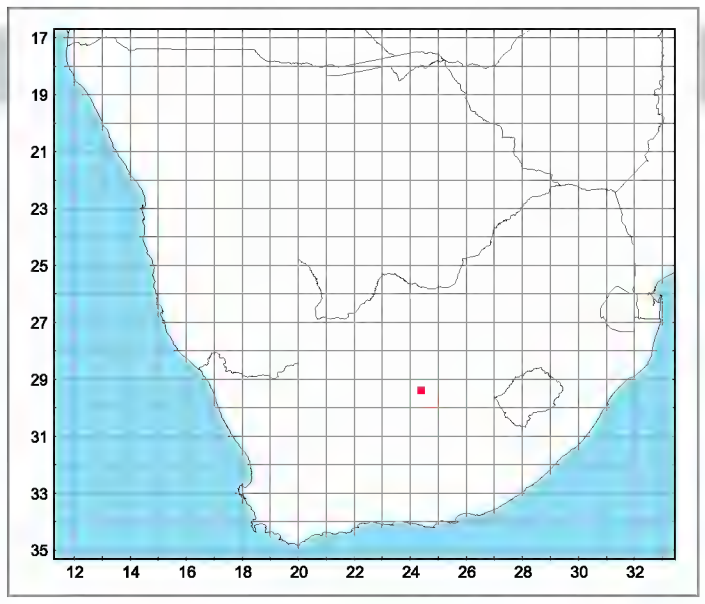
Temporal activity: Observed active by DBRU personnel in bright sunshine during daytime (mid-morning) in the early winter dry season (May).

Bioregions South Africa: S Dry Highveld Grassland: Besemkaree Koppies Shrubland (Gh 4); S Drakensberg Grassland: Stormberg Plateau Grassland (Gd 3) (both Grassland Biome).

Assessment rationale: EOO = 105 km^2 (underestimated); may be poorly represented in collections due to restricted range and seasonal activity at a time of the year when little sampling is conducted for dung beetles; assessment of conservation status not possible owing to severely limited information; transformation in occupied vegetation units: 3% (Gh 4), 9% (Gd 3); currently would qualify for an IUCN threat category, but small range would be a collecting artefact; assessed as Data Deficient (DD).

Conservation measures: To assess conservation status, it is necessary to conduct a survey in the highlands of the Eastern Cape during early winter to determine its EOO, AOO and ecological associations; although not currently known to be protected in any reserve, the extremely small known range has been little transformed.





Onitis longitibialis

Ferreira, 1977

No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Cape Province: Nº 1024, Hopetown (30 km N)' [South Africa].
Taxonomy: Accepted Group XI species; known only by the holotype male.
Distribution: Known only from the type locality in an area of arid shrub/grassland in central South Africa.
Locality data: Altitude: 1 222 m; annual rainfall: 353 mm; annual temperature (max. + min. /2): 17.6°C (N=1).
Habitat: No quantitative assessment; DBRU collection record: a single known individual on sand (1) in pasture (1).
Food types: No quantitative assessment; DBRU collection record: one individual collected from either cattle or horse dung.
Temporal activity: Flight activity in darkness during the late summer rainy season (Mar.).
Bioregions South Africa: Upper Karoo (NKu) (Nama Karoo Biome).
Assessment rationale: EOO unknown; represented in museums by only the holotype specimen; as other Group XI members show a bias to omnivore or monogastric herbivore dung, recent discovery and rarity of collection may be related to dung type specialisation in an area where monogastric herbivores are now uncommon; however, EOO and ecological associations essentially unknown; assessed as Data Deficient (DD).
Conservation measures: To assess conservation status, a quantitative survey is required to determine the EOO, AOO and ecological associations; not currently known to be protected in any reserve although the type locality lies in an area in which the vegetation cover is little transformed.

Onitis mendax

Gillet, 1918

= *Onitis cerrutii* Müller, 1949
= *Onitis janssenii* Gomes Alves, 1954

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. mendax*: 'Afrique Orientale: Sud-Ouest du Volcan Gurui' [SW of Gurui Volcano, Tanzania]; *O. cerrutii*: 'Rhodesia meridionali. Loc. class.: Gatooma' [Zimbabwe]; *O. janssenii*: 'Moçambique:... Mutuali' [Mozambique].

Taxonomy: Accepted Group XIX species; limited sexual dimorphism (legs), prominence of characters varies with body size.

Distribution: Widespread, but patchy occurrence in moist savanna regions from southern to E Africa due to soil and dung type specialisation: N South Africa, Botswana, Namibia; Zimbabwe, Mozambique, Tanzania, Kenya.

Locality data (mean ± SD, range): Altitude: 657 ± 449, 110–1 850 m; annual rainfall: 628 ± 145, 374–1 042 mm; annual temperature (max. + min. /2): 21.5 ± 1.8, 13.4–23.2°C (N=39).

Habitat: No quantitative assessment; DBRU collection records entirely from finer-grained soils: clay (1), sandy clay loam (7), sandy loam (6); primarily in open shrub/woodland (8), grassland (1).

Food types: No quantitative assessment; DBRU collection records strongly biased to monogastric herbivore dung: elephant (9), square-lipped (white) rhinoceros (4); one record on ruminant herbivore dung: buffalo.

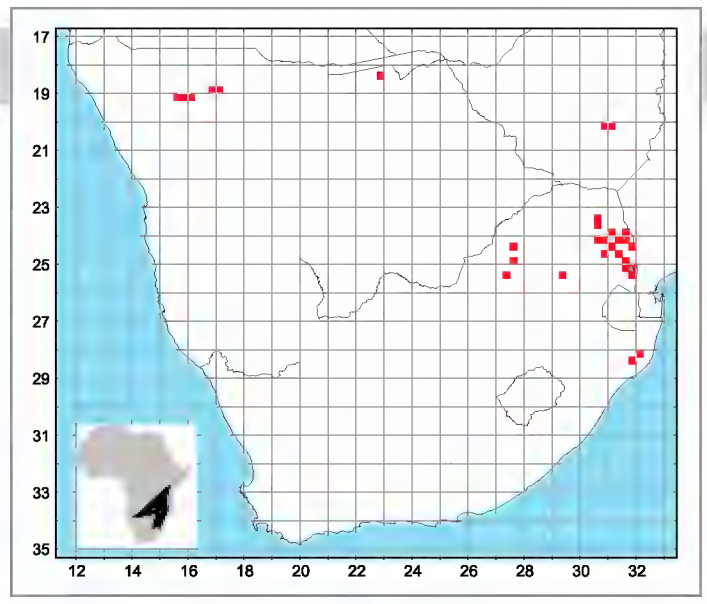
Temporal activity: Diel flight activity in darkness (crepuscular: dusk/dawn and nocturnal) (Caveney et al. 1989) in the summer rainy season (Oct. to Apr.); attracted to light.

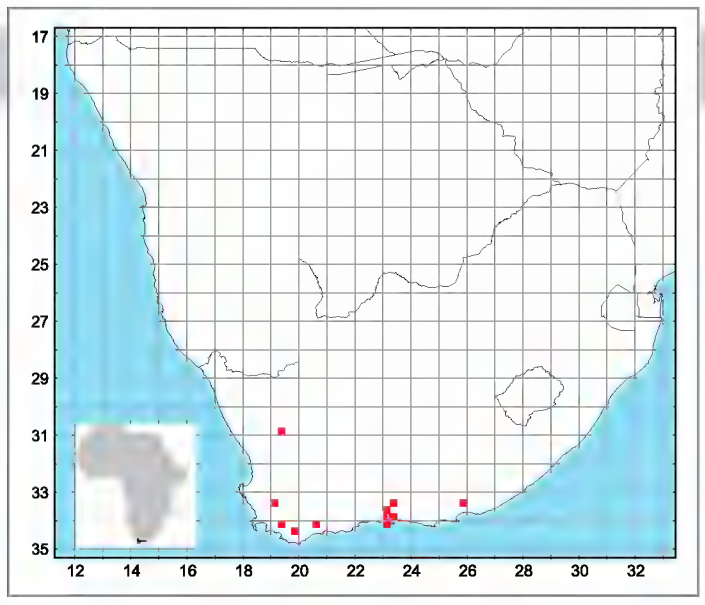
Ecoregions Namibia, Botswana, Zimbabwe: Angolan Mopane Woodlands (AT0702), Zambezian Baikiaea Woodlands (AT0726), Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Central Bushveld (SVcb), Lowveld (SVl), Mopane (SVmp) (Savanna Biome).

Assessment rationale: EOO = 2 759 790 km^2 (gross estimate); AOO much smaller; range fragmented due to range contraction of monogastric herbivores, particularly elephant and rhinoceros; occurrence centred on game reserves or unproclaimed areas in which elephants still occur on finer-grained soils (67% of available records from reserves, n=37/55); recent records from dung of re-introduced elephant or rhinoceros (South Africa: Thabazimbi area, Loskop Dam Nature Reserve) suggest low density relict populations still occurred in these areas; assessed as Least Concern (LC) owing to wide range and occurrence in many reserves.

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; observations suggest conservation status would be dependent on the continuing protection of elephants and rhinoceros in reserves; protected in Kruger National Park, Hluhluwe–iMfolozi Game Reserve (South Africa), Lake Mutirikwe Game Reserve (Zimbabwe), Etosha National Park (Namibia), Meru National Reserve, Masai Mara Game Reserve (Kenya).





Onitis minutus

van Lansberge, 1875b

No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'l'Afrique méridionale…..le sud de l'Afrique' [southern Africa].

Taxonomy: Accepted Group VII species; limited sexual dimorphism (legs), prominence of characters varies with body size.

Distribution: Lowlands in the winter and bimodal rainfall regions along the S coastal region, South Africa; also one old record from Loeriesfontein to the arid N; only in Western and Eastern Cape; citations from the old provinces of Transvaal and Natal are errors.

Locality data (mean ± SD, range): Altitude: 393 ± 353, 26–1 100 m; annual rainfall: 386 ± 98, 148–484 mm; annual temperature (max. + min. /2): 16.9 ± 1.1, 14.8–18.2°C (N=11).

Habitat: No quantitative assessment; DBRU collection records from tuft grassland, scrub and shrubland in the Eastern Cape (single records), but only in disturbed habitats in the Western Cape (grass and lucerne pasture, fallow crop fields); recorded on sandy loam (4) with single records on sand, sandy clay loam and clay.

Food types: No quantitative assessment; DBRU collection records entirely from cattle dung (7).

Temporal activity: In Western Cape: diurnal flight activity peaking in early afternoon (during May at Gouda); primarily active during autumn (May, June), but also recorded in spring (Oct.).

Bioregions South Africa: In the W: Shale Renosterveld (FRs) (Fynbos Biome); in the E: Sandstone Fynbos (FFs) (Fynbos Biome), Albany Thicket Biome (AT); in the N: Hantam Karoo (SKt 2) (Succulent Karoo Biome) (Loeriesfontein).

Assessment rationale: EOO = 70 125 km^2; widespread, but not commonly collected; assessment of conservation status difficult owing to limited information; readily attracted to cattle dung in farmland and apparently tolerant of habitat disturbance; significance, if any, of regional differences in shrubland vs disturbed habitat association is unclear, but transformation in W: 80–90% (FRs); in E: 8–28% (FFs); assessed as Data Deficient (DD).

Conservation measures: To assess conservation status, it is necessary to conduct a survey along the southern coastal lowlands of the Western and Eastern Cape during autumn to determine its EOO, AOO and ecological associations; also, if these differ between the Western and Eastern Cape; not currently known to be protected in any reserve.

Onitis mniszechi

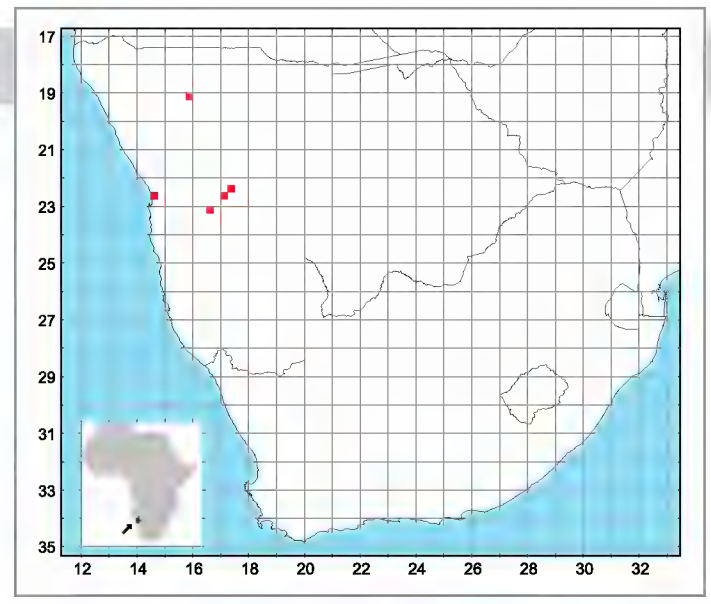
van Lansberge, 1875b

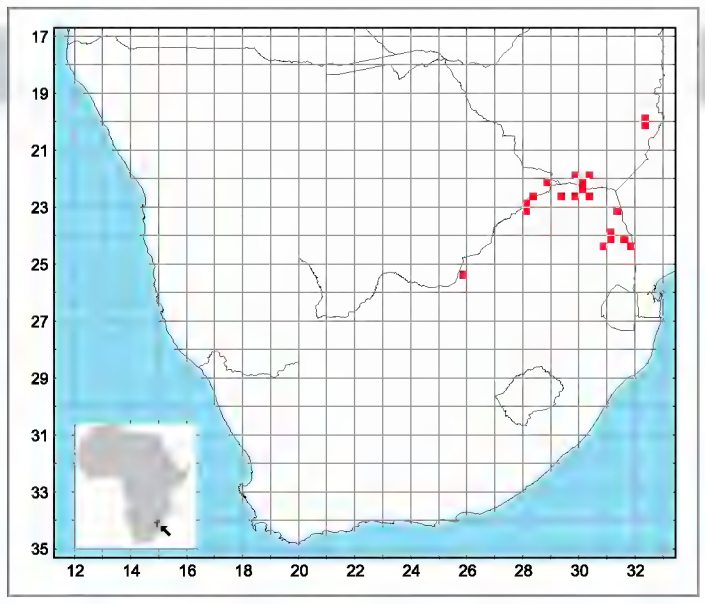
No synonyms

Global: DD (see IUCN Red List – DD)
Endemic: Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Damara' [Damaraland, N Namibia].
Taxonomy: Accepted Group XVIII species; limited sexual dimorphism (head, legs), prominence of characters varies with body size.
Distribution: Arid savanna in N Namibia, mostly in uplands; one record on cool coastline.
Locality data (mean ± SD, range): Altitude: 1 236 ± 707, 58–1 805 m; annual rainfall: 265 ± 147, 14–391 mm; annual temperature (max. + min. /2): 18.7 ± 2.6, 15.9–22.2°C (N=5).
Habitat: No quantitative assessment; one DBRU record from sand, one from sandy clay loam in scrub or low shrubland.
Food types: No quantitative assessment; one DBRU record from cattle dung, one from zebra dung.
Temporal activity: Flight activity in darkness during the late summer rainy season (Feb. to Apr.).
Ecoregions Namibia: N Kalahari Xeric Savanna (AT1309), Namibian Savanna Woodlands (AT1316), Angolan Mopane Woodlands (AT0702); also Namib Desert (AT1315).
Assessment rationale: EOO = 67 800 km²; fairly wide range, but rare in collections, possibly due to specialisation on dung of monogastric herbivores whose ranges have contracted or whose dung types are not well represented by domestic livestock in farm rangeland resulting in low population density; assessed as Data Deficient (DD).
Conservation measures: To assess conservation status, it is necessary to conduct a survey in dry upland savanna and coastal regions of N Namibia to determine its EOO, AOO and ecological associations; suspected dung specialisation may mean presence of equids is essential for its conservation; protected in Etosha National Park (Namibia).





Onitis obenbergeri

Balthasar, 1942

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Transvaal, Linokana' [Linokana, North-West Province, South Africa].

Taxonomy: Accepted Group XVII species; limited sexual dimorphism (legs), prominence of characters varies with body size.

Distribution: Hot, dry lowlands below the E escarpment and up dry river valleys of the Limpopo and Sabi; N South Africa, SE Zimbabwe, E Botswana.

Locality data (mean ± SD, range): Altitude: 533 ± 228, 274–1 370 m; annual rainfall: 431 ± 104, 304–656 mm; annual temperature (max. + min. /2): 22.3 ± 1.1, 18.1–23.6°C (N=26).

Habitat: No quantitative assessment; DBRU collection records suggest a bias to coarse-grained soils: sandy loam (11), sand (5), in open woodland (15), especially mopane.

Food types: At Phalaborwa: strong bias to monogastric herbivore dung; much lower attraction to dung of ruminant herbivores and omnivores, elephant (196), pig (35), cattle (14); DBRU collection records: mainly cattle dung (16), also elephant (1), donkey (2), horse (2).

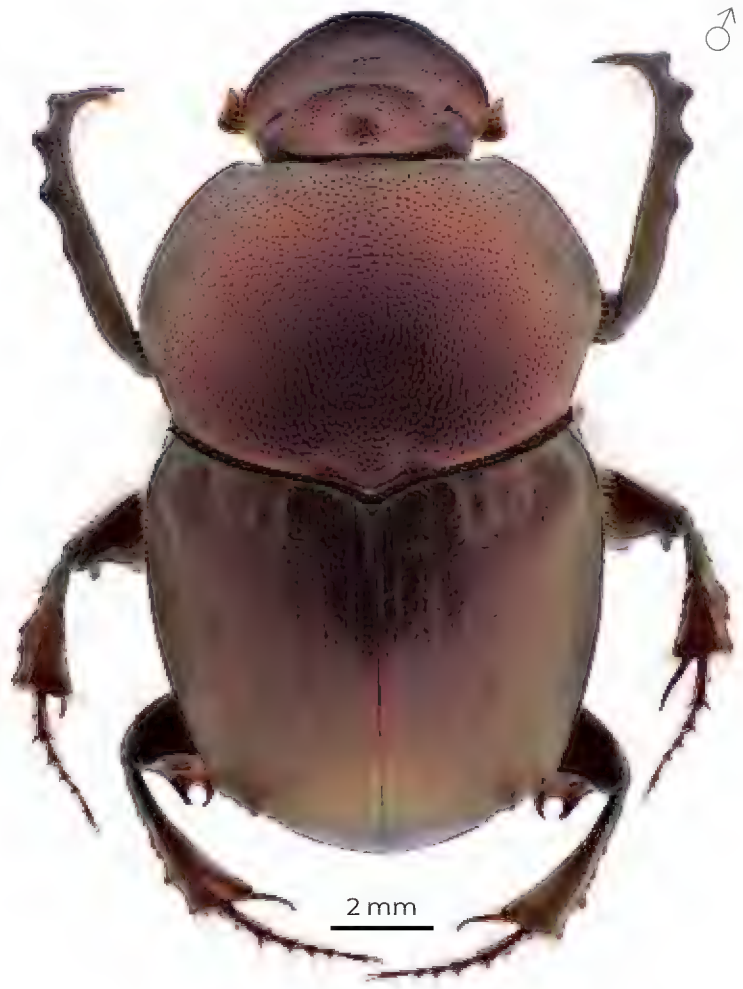
Temporal activity: Flight activity in darkness during the summer rainy season (Oct. to Apr.); at Phalaborwa: sensitive to rainfall events, warm evenings after heavy rain (128), after light rain (96), warmer evening under dry conditions (24).

Ecoregions Botswana, Zimbabwe: Dry S Zambezian and Mopane Woodlands (AT0725); also margins of Southern African Bushveld (AT0717).

Bioregions South Africa: Mopane (SVmp); marginal in Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome).

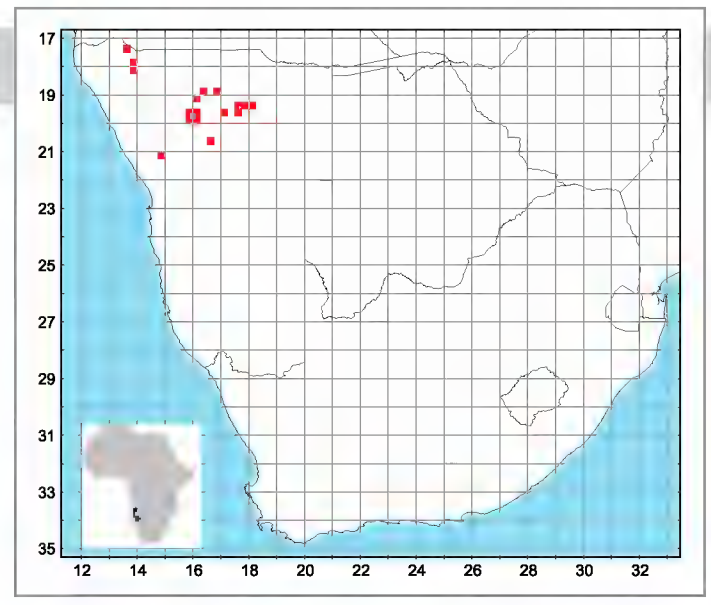
Assessment rationale: EOO = 59 050 km^2; strong association with woodlands and monogastric herbivore dung could result in lower population density in farmland; particularly in South Africa where its range is centred on a bioregion that has been 1–20% transformed, mainly by cultivation; however, not currently threatened due to widespread persistence of woodland across a wide range; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on habitat associations and by measurements of population density in response to woodland clearance and differences in dung type diversity between reserves and farmland; protected in Kruger National Park (South Africa).



Onitis obscurus

van Lansberge, 1886



No synonyms

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Humpata' [SW Angola].

Taxonomy: Accepted Group XVII species; limited sexual dimorphism (legs), prominence of characters varies with body size.

Distribution: N Namibian plateau; moister upland areas at E edge of Kaokoveld (Namibia); SW Bié Plateau, SW Angola.

Locality data (mean ± SD, range): Altitude: 1 299 ± 203, 831–1 627 m; annual rainfall: 478 ± 143, 282–813 mm; annual temperature (max. + min. /2): 20.4 ± 1.7, 17.1–23.0°C (N=21).

Habitat: No quantitative assessment; DBRU collection records from finer-grained soils: clay (2), sandy clay loam (4), sandy loam (4), primarily in open shrub-woodland (8); one record from a harvested crop field.

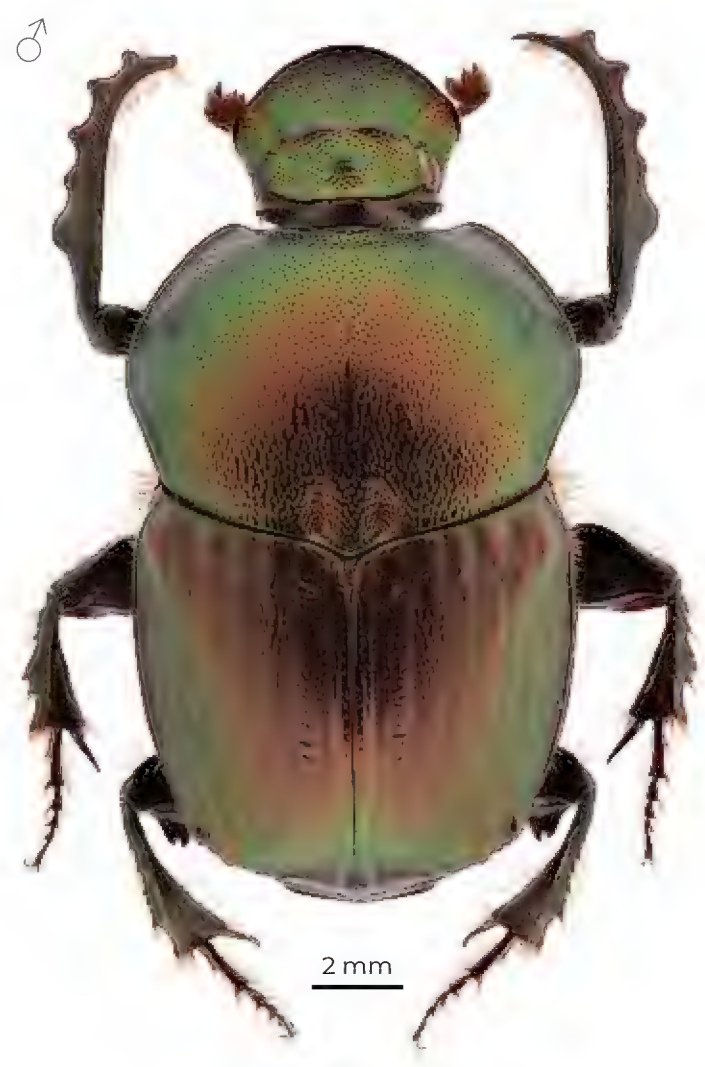
Food types: No quantitative assessment; DBRU collection records from various dung types in farmland: cattle (7), donkey (1), and reserves: elephant (1), zebra (1).

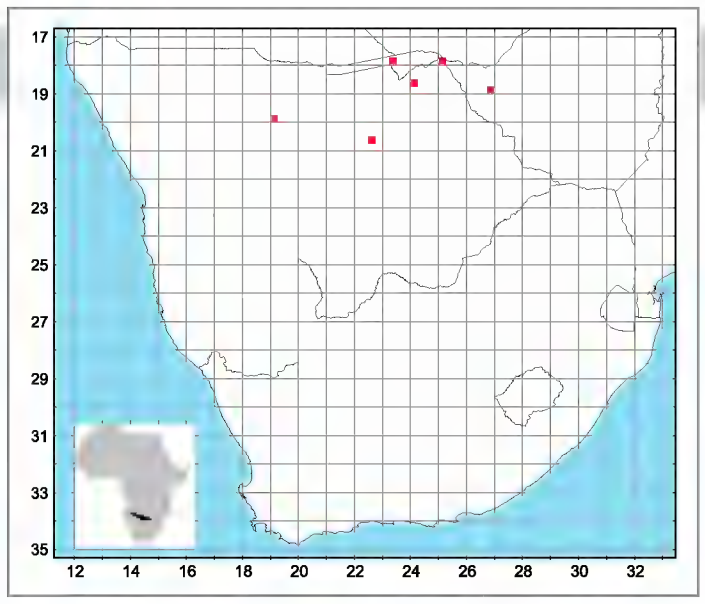
Temporal activity: Flight activity in darkness during the late summer rainy season (Dec. to Apr.).

Ecoregions Namibia: Angolan Mopane Woodlands (AT0702), N Namibian Savanna Woodlands (AT1316); marginal occurrence in three other ecoregions.

Assessment rationale: EOO = 157 030 km^2; AOO possibly smaller if associated with woodland; not recently re-recorded (1974) at its type locality, which has been widely converted to grassland; however, not currently threatened as wooded farmland is widespread across its range where it is attracted to the dung of domestic livestock; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; it should also be determined if population density is adversely influenced by clearance of woodland; protected in Etosha National Park (Namibia).





Onitis orthopus

van Lansberge, 1875b

= *Onitis orthopus* var. *tanganyikensis* Janssens, 1937

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. orthopus*: 'Caffrerie intérieure (N'Gami)' [SE African interior: Lake Ngami, Botswana]; var. *tanganyikensis*: 'Tanganyika' [Tanzania].

Taxonomy: Accepted Group XIX species; limited sexual dimorphism (legs), prominence of characters varies with body size; taxonomic status of var. *tanganyikensis* should be re-examined; assessment below only for southern African *O. orthopus*.

Distribution: Probably range restricted to E Angola, NE Namibia, N Botswana and W Zimbabwe due to specialisation to deep sands; possibly also northeastwards to Tanzania if var. *tanganyikensis* does not deserve species status.

Locality data (mean ± SD, range): Altitude: 1 056 ± 177, 871–1 362 m; annual rainfall: 618 ± 117, 414–813 mm; annual temperature (max. + min. /2): 21.4 ± 1.4, 18.5–22.4°C (N=7).

Habitat: No adequate quantitative assessment; on deep sand in N Botswana: primarily sampled from open woodland (92), few from open shrubland on lacustrine sands (4); DBRU collection records on sand (3) and sandy loam (1) in open shrub/woodland (3) and riverine grass (1).

Food types: In Botswana: strong bias to monogastric herbivore dung: elephant (80); also dung of pig (15); few on sheep dung (1); absent from cattle dung (0) and carrion (chicken livers) (0); DBRU collection records on elephant (3) and cattle (1) dung.

Temporal activity: Flight activity in darkness during the summer rainy season (Nov., Dec.).

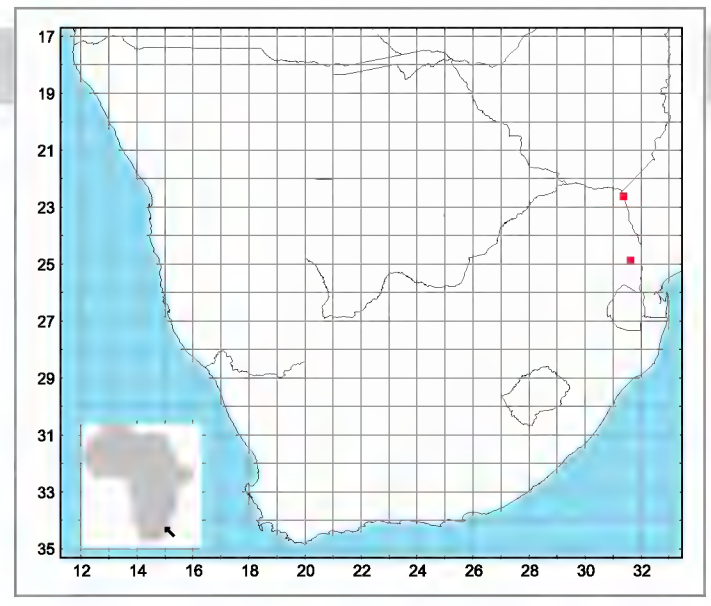
Ecoregions Namibia, Botswana, Zimbabwe: Zambezian Baikiaea Woodlands (AT0726); margins of three adjacent woodland ecoregions.

Assessment rationale: EOO = 281 070 km^2 (possibly underestimated); measured EOO and AOO restricted to moist sands of the central mega-Kalahari system where it shows a strong bias to elephant dung and possibly to woodland; large parts of the region officially under protection although elephant population density was recently radically reduced in SE Angola, but is now on the increase; currently assessed as Least Concern (LC) on basis of protection in Botswana and Zimbabwe.

Conservation measures: Assessment of conservation status would be improved by quantitative data on habitat associations, particularly if there are any effects of woodland clearance; observations and available data suggest conservation status would be dependent on the continuing protection of elephants in woodland on deep sand; a survey is necessary to determine its present conservation status in Bicuar National Park and SE Angola (see notes under *Platyonitis bicuariensis* Ferreira, 1976); protected in Chobe (Botswana) and Hwange (Zimbabwe) national parks.

Onitis paraconfusus

Ferreira, 1976a



No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Transvaal : nº 1046, KNP, Skukuza' [Skukuza, Kruger National Park, South Africa].

Taxonomy: Accepted Group XIX species; limited sexual dimorphism (legs), prominence of characters varies with body size.

Distribution: Currently known only from dry, lowland savanna of the Kruger National Park in NE South Africa, but likely also occurring on the S Mozambique Coastal Plain, possibly also SE Zimbabwe.

Locality data (mean ± SD, range): Average altitude: 377 ± 139, 278–475 m; average annual rainfall: 578 ± 110, 500–655 mm; average annual temperature (max. + min. /2): 22.4 ± 0.6, 21.9–22.8°C (N=2).

Habitat: No quantitative assessment; not known, but one record from Nyandu Bush that is characterised by open woodland on deep sand.

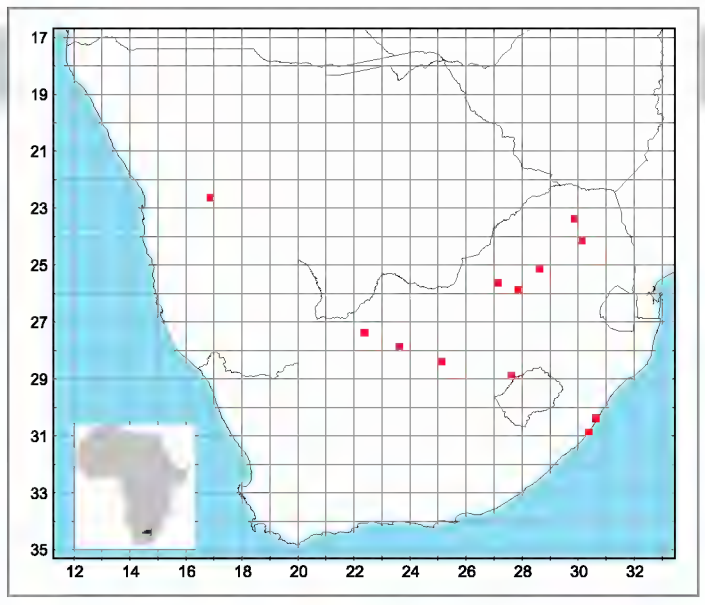
Food types: No quantitative assessment; one DBRU collection record from elephant dung.

Temporal activity: Flight activity during darkness in the summer rainy season (Nov., Mar.).

Bioregions South Africa: Mopane (SVmp), Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 1 950 km^2 (underestimated); AOO would be smaller than EOO if sand specialisation is supported by quantitative data; distribution would be susceptible to elephant range contraction if it is a coarse-dung specialist like its closest relatives; however, currently, ecologically very poorly known and assessed as Data Deficient (DD).

Conservation measures: A quantitative survey is required to determine the EOO, AOO and ecological associations; continuing conservation of monogastric herbivores such as elephant and rhinoceros would be essential for the conservation of this species if it proves to be a coarse-dung specialist; both known localities protected in the Kruger National Park, South Africa.



Onitis parainflaticollis

Ferreira, 1977

No synonyms

Global: DD (see IUCN Red List – DD)
Endemic: RSA, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'South Africa. Orange Free State: Ficksburg, Farm Op die Wal' [Free State, South Africa].

Taxonomy: Accepted Group XII species; limited sexual dimorphism (prothoracic disc, legs), prominence of characters varies with body size.

Distribution: Scattered occurrence over a wide range in South Africa, mostly on drier, NW, upland savanna, but also on moist coastal hills; also central uplands of Namibia.

Locality data (mean ± SD, range): Altitude: 1 115 ± 497, 88–1 726 m; annual rainfall: 631 ± 228, 314–979 mm; annual temperature (max. + min. /2): 18.3 ± 1.2, 15.3–19.7°C (N=12).

Habitat: No quantitative assessment; one DBRU collection record from sandy loam in pasture around a granite outcrop; possible bias to sandy soils in open vegetation requires quantitative support.

Food types: No quantitative assessment; one DBRU collection record from cattle dung, but rarity may indicate specialisation to less common dung types; two recent records from fresh dung in hyrax middens in Namibia.

Temporal activity: Diel periodicity unknown, but, presumably, flies during darkness like most other warm temperature *Onitis* species; recorded in the summer rainy season (Dec. to Apr.).

Ecoregions Namibia: NW Kalahari Xeric Savanna (AT1309).

Bioregions South Africa: Primarily Central Bushveld (SVcb), Eastern Kalahari Bushveld (SVk) (Savanna Biome); also Mesic Highveld Grassland (Gm) (Grassland Biome) and Indian Ocean Coastal Biome (CB).

Assessment rationale: EOO = 116 085 km^2; ecologically poorly known; AOO possibly restricted due to dung specialisation, like some other *Onitis* species; no observations to support specialisation to dung of monogastric herbivores whose ranges have contracted (zebra, elephants, rhinoceros) with scattered replacement by domestic livestock (horses, donkeys) at low population density; recent observations from hyrax dung may suggest an alternative type of dung specialisation; rarity in collections suggests *O. parainflaticollis* is uncommon across its entire wide range; however, there are no data to support local and regional threats; currently assessed as Data Deficient (DD).

Conservation measures: Quantitative data on ecological associations, particularly dung type associations, is required to assess conservation status as these may strongly influence both EOO and AOO, more so than soil and vegetation type; protected in several nature reserves, including Lekgalameetse, Rustenburg and Vernon Crookes.

Onitis pecuarius

van Lansberge, 1875b

= *Onitis viridulus* Boheman, 1857, *sensu* Péringuey, 1901 (*pars* South Africa)

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *Onitis pecuarius*: 'Cap de Bonne-Espérance, Caffrerie' [Cape of Good Hope and SE South Africa]; *O. viridulus sensu* Péringuey: 'Natal (Durban), Cape Colony (Seymour)...' [South Africa].

Taxonomy: Accepted Group III species; limited sexual dimorphism (legs), prominence of characters varies with body size; synonym requires re-examination as cited type localities in '...Southern Rhodesia (Victoria Falls, Buluwayo)' [Zimbabwe], undoubtedly relate to one or more species other than *O. pecuarius*.

Distribution: Moist E regions of the Highveld and coast of South Africa from Limpopo through KwaZulu-Natal to the Eastern Cape; records from Zimbabwe are erroneous.

Locality data (mean ± SD, range): Altitude: 876 ± 669, 0–3 218 m; annual rainfall: 730 ± 181, 390–1 065 mm; annual temperature (max. + min. /2): 16.7 ± 2.4, 4.8–21.5°C (N=116).

Habitat: Little quantitative data; DBRU collection records primarily on finer-grained soils, sand (2), sandy loam (10), sandy clay loam (26), clay (1), primarily in pasture/grassland (35), open woodland (1); population density greater in modified habitats at Carolina (Jan. 2001), natural *Themeda* grassland (16), fallow crop fields (34), improved Kikuyu pasture (68).

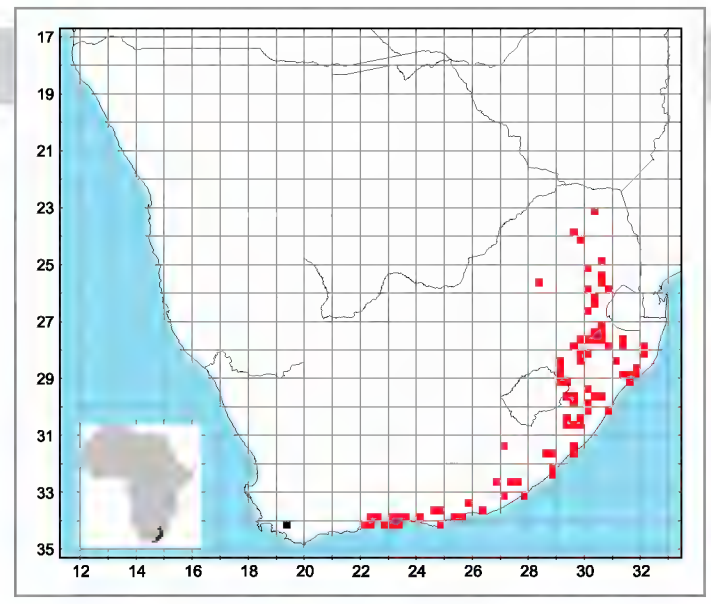
Food types: No quantitative assessment; DBRU collection records primarily from cattle dung (53), horse dung (1).

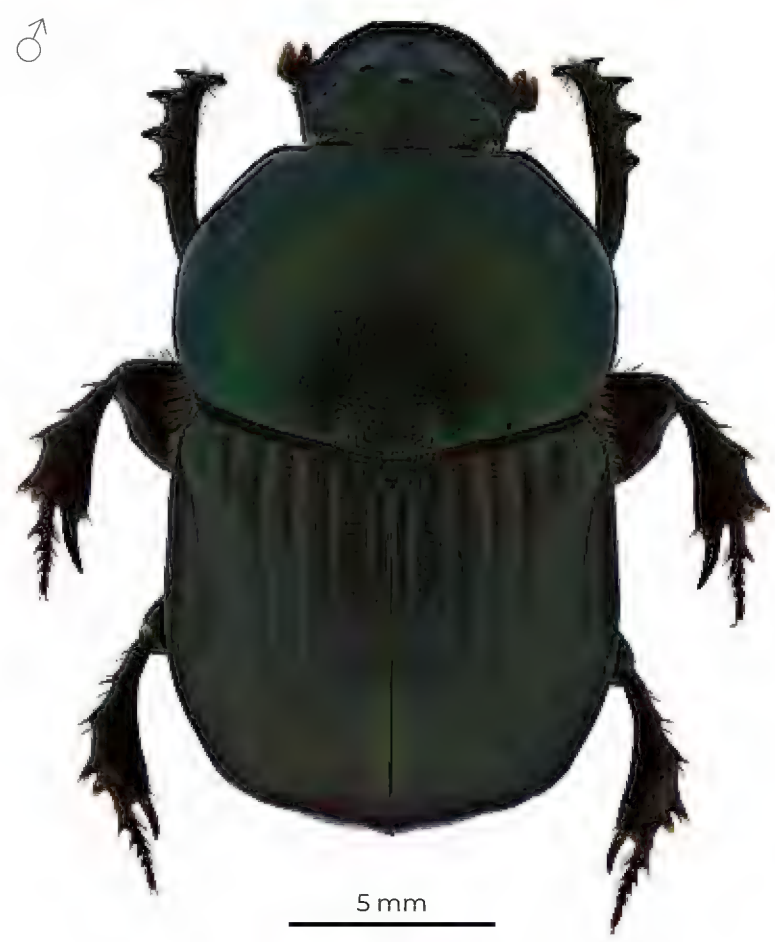
Temporal activity: Diel flight activity in darkness (crepuscular: dusk/dawn) (Caveney et al. 1989) during the summer rainy season (Oct. to May).

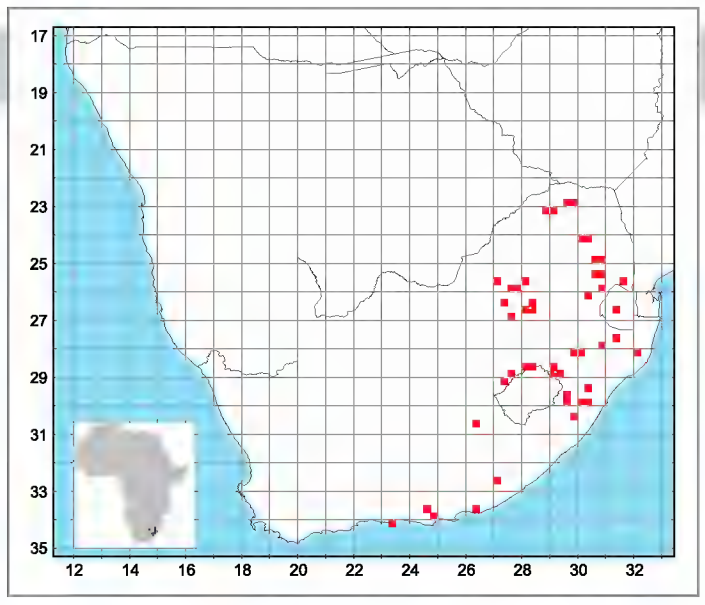
Bioregions South Africa: In the E: E Mesic Highveld Grassland (Gm), E Drakensberg Grassland (Gd), N and E Sub-Escarpment Grassland (Gs) (Grassland Biome); Indian Ocean Coastal Belt Biome (CB); in the S: pastures in Albany Thicket (AT), Afrotemperate Forest (FO) Biomes, Shale Renosterveld (FRs) (Fynbos Biome).

Assessment rationale: EOO = 198 180 km^2; abundant in both natural and modified grasslands; restriction of collection records to moist pasture along the S coast may indicate range expansion in response to clearance of natural woody vegetation that characterises the regional biomes (Albany Thicket; Fynbos, Afrotemperate Forest); one observation (black square) in isolated irrigated pasture in the Western Cape; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; however, apparently resilient to vegetation transformation within an agro-ecosytem; protected in Ithala and Hluhluwe–iMfolozi game reserves.







Onitis perpunctatus

Balthasar, 1963c

No synonyms

Global: LC
Endemic: RSA, Eswatini

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Natal, Distr. Richmond, Indaleni' [Indaleni, KwaZulu-Natal, South Africa].

Taxonomy: Accepted Group VII species; limited sexual dimorphism (legs), prominence of characters varies with body size; very closely related to *O. caffer* Boheman, 1857, but differs in seasonality.

Distribution: Primarily open vegetation in moist uplands along Soutpansberg, NW edge of Highveld and edge of E escarpment in the N descending to coastal lowlands in the S; unclear if disjunction between E escarpment and NW edge of Highveld is real or a collection artefact; South Africa, Eswatini.

Locality data (mean ± SD, range): Altitude: 1 268 ± 503, 7–1 958 m; annual rainfall: 741 ± 136, 390–1 157 mm; annual temperature (max. + min. /2): 16.5 ± 2.0, 13.1–22.1°C (N=57).

Habitat: No quantitative soil assessment; DBRU collection records from finer-grained soils: sandy loam (4), sandy clay loam (6); on the Wolkberg: primarily in forest at ± 900 m and ± 1 375 m (3.9 per sample), few in grassland at ± 1 350 m (0.1); however, DBRU collection records primarily from pasture (8), but also forest (1).

Food types: On the Wolkberg: slight bias to pig dung at ± 900 m to ± 1 375 m (4.8 per sample), compared to cattle dung (3.0); however, DBRU collection records entirely from cattle dung (11).

Temporal activity: Flight activity in darkness during the summer rainy season (Nov. to May); the only summer-active member of Group VII in South Africa.

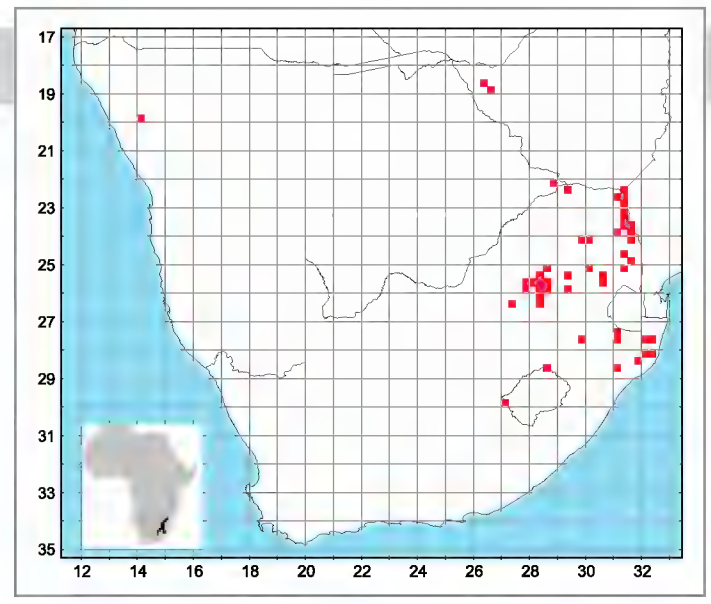
Bioregions South Africa: In the N: primarily, N and E edge of Mesic Highveld Grassland (Gm), N Sub-Escarpment Grassland (Gs) (Grassland Biome); in the S: primarily Albany Thicket Biome (AT); marginal occurrence in four other bioregions.

Assessment rationale: EOO = 96 210 km^2; although quantitative data from the Wolkberg at ± 1 400 m show much greater abundance in forest compared to grassland, nevertheless, widely collected in pasture and grassland across a large EOO and AOO; therefore, not considered to be threatened and assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations to resolve apparent contradictions between qualitative and current quantitative data; protected in various game and nature reserves, including Abe Bailey, Suikerbosrand, Ithala, Hluhluwei–iMfolozi.

Onitis picticollis

Boheman, 1857



No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'juxta fluvium Limpopo' [near Limpopo River, southern Africa].

Taxonomy: Accepted Group III species; limited sexual dimorphism (legs), prominence of characters varies with body size.

Distribution: Southern African savannas and grassland; N South Africa, N Namibia, E Botswana, Zimbabwe, Mozambique; report from Tanzania requires validation.

Locality data (mean ± SD, range): Altitude: 871 ± 534, 55–1 783 m; annual rainfall: 657 ± 163, 298–1 136 mm; annual temperature (max. + min. /2): 19.7 ± 2.9, 13.8–25.2°C (N=65).

Habitat: No quantitative assessment; DBRU collection records on sand (4), sandy loam (5), sandy clay loam (5) and clay (2) in pasture/grassland (5) and open shrub/woodland (11).

Food types: No quantitative assessment; DBRU collection records dominated by dung of monogastric herbivores (13): elephant (9), hooked-lipped (black) (1) and square-lipped (white) rhinoceros (2), horse (1); fewer on dung of ruminant herbivores (7): cattle (6), buffalo (1).

Temporal activity: Flight activity in darkness, primarily in the summer rainy season (Oct. to May); attracted to light.

Ecoregions Namibia, Zimbabwe: Namibian Savanna Woodlands (AT1316); Zambezian and Mopane Woodlands (AT0725).

Bioregions South Africa: Savanna (SV) and N of Grassland (G) biomes: Lowland (SVl), Mopane (SVmp); also straddling the margins of Central Bushveld (SVcb), Dry Highveld Grassland (Gh), Mesic Highveld Grassland (Gm); also N Sub-Escarpment Grassland (Gs).

Assessment rationale: EOO = 327 800 km^2 (underestimated); found on a range of soil types in open and partially shaded vegetation types; however, a large number of available records are from game and nature reserves (60%, n=44/73), presumably due to bias to dung of monogastric herbivores; smaller number of records on cattle dung in farmland may reflect lower population density; however widespread in reserves and farmland, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; particularly a study to determine relative population densities where monogastric herbivores are either present (many reserves) or absent (often in farmland); protected in Kruger National Park (South Africa).

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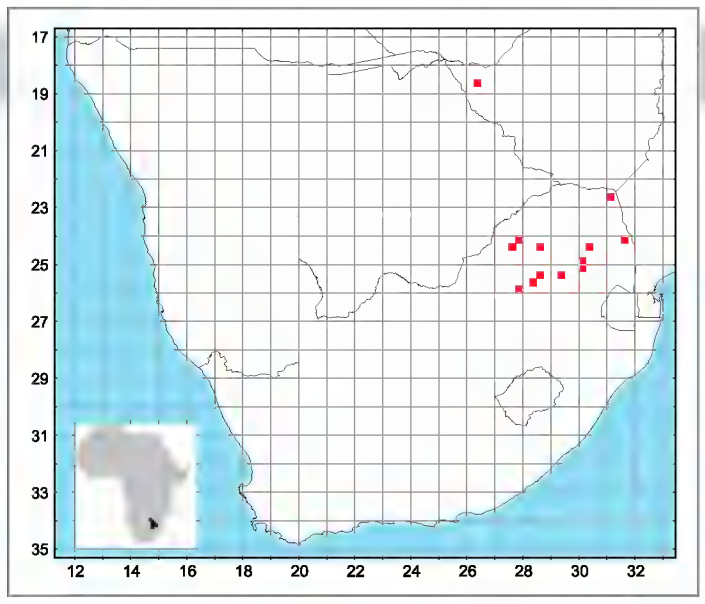


Onitis pseudosetosus

Ferreira, 1976a

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Rhodesia : nº 1310, Wankie N.P. (Nr. Sinamatella)' [Hwange National Park, Zimbabwe].

Taxonomy: Accepted Group XI species; limited sexual dimorphism (legs), prominence of characters varies with body size.

Distribution: Moist savanna along the Waterberg and N edge of Highveld, South Africa; further scattered records in lowveld savanna of South Africa N to Zimbabwe; also cited from Zambia, Kenya.

Locality data (mean ± SD, range): Altitude: 1 063 ± 312, 226–1 448 m; annual rainfall: 639 ± 64, 503–736 mm; annual temperature (max. + min. /2): 19.4 ± 1.9, 17.1–23.1°C (N=18).

Habitat: No adequate quantitative assessment; in open woodland at Leeuwfontein Nature Reserve: sampled on loamy sand (40), sandy loam (48), stony sandy loam (29); one DBRU collection record on sandy loam.

Food types: No quantitative assessment; sampled in relative abundance to composite pig/cattle bait in Leeuwfontein Nature Reserve (117) where a zebra population was present.

Temporal activity: Flight activity in darkness during the summer rainy season (Nov. to Feb.).

Ecoregions Zimbabwe: Zambezian and Mopane Woodlands (AT0725).

Bioregions South Africa: Central Bushveld (SVcm), Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 191 355 km² (southern Africa only; underestimated); data insufficient to determine if ecological separation from the sympatric Group XI relative, *O. aeruginosus*, in Hwange National Park is related to edaphic, climatic or some other ecological factor; assessed as Least Concern (LC) owing to wide distribution and protection in various reserves.

Conservation measures: Assessment of conservation status would be improved by a quantitative survey to determine the full EOO and the effect on AOO of possible ecological associations, particularly those with soil and dung type; protected in Hwange National Park (Zimbabwe), Leeuwfontein Nature Reserve (South Africa).

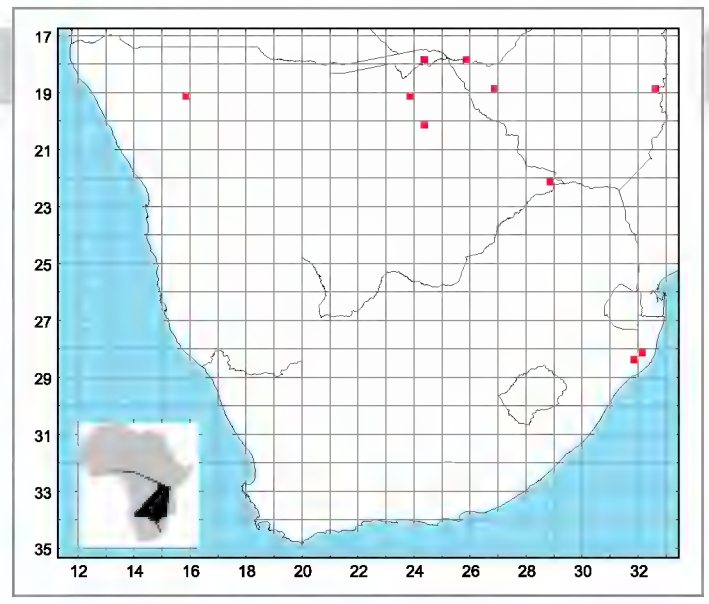
Onitis robustus

Boheman, 1857

= *Onitis zambesianus* Péringuey, 1896
= *Onitis lunaris* Kolbe, 1897

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: *O. robustus*: 'prope fluvium Limpopo' [close to Limpopo River, southern Africa]; *O. zambesianus*: 'Zambezia (Manica)' [central Mozambique]; *O. lunaris*: 'Im westlichen Theile der Issango-Ebene nordlich vom Albert-Edward See' [in the western parts of the Semliki Valley north of Lake Albert, Democratic Republic of the Congo (DRC); Semliki = Issango river of Emin Pasha].

Taxonomy: Accepted Group IX species; limited sexual dimorphism (legs), prominence of characters varies with body size.

Distribution: S to E to W African moist savanna: patchy occurrence, primarily in game reserves due, especially, to dung type specialisation: N South Africa, N Botswana, N Namibia, Angola, Zimbabwe, Mozambique, Democratic Republic of the Congo (DRC), Tanzania, Kenya, Côte d'Ivoire; also reported from Rwanda, Uganda.

Locality data (mean ± SD, range): Altitude: 691 ± 401, 59–1 377 m; annual rainfall: 697 ± 235, 329–1 136 mm; annual temperature (max. + min. /2): 22.2 ± 1.9, 17.3–25.2°C (N=15).

Habitat: No quantitative assessment; DBRU collection records entirely from finer-grained soils: clay (2), sandy clay loam (2), sandy loam (3), in open shrub/woodland (6).

Food types: No quantitative assessment; DBRU collection records dominated by monogastric herbivore dung: elephant (10), square-lipped (white) rhinoceros (3); one record from ruminant herbivore dung: buffalo.

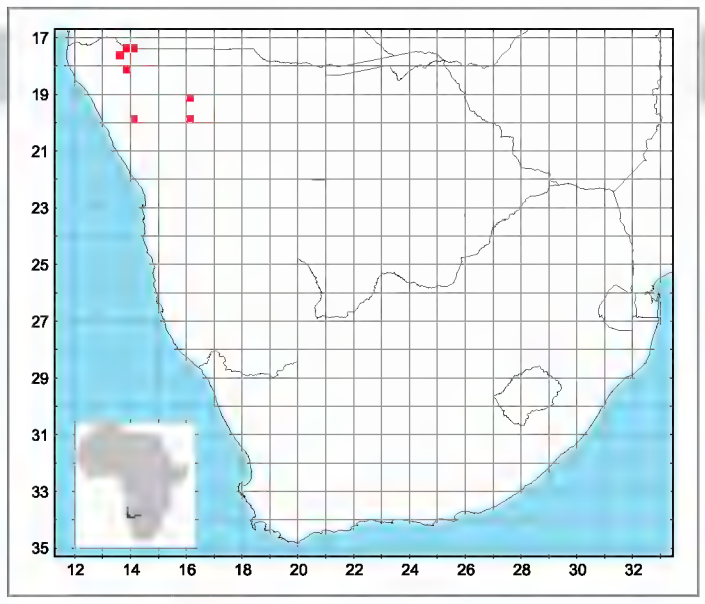
Temporal activity: Flight activity in darkness, primarily in the summer rainy season (Oct. to May); attracted to light.

Ecoregions Namibia, Botswana, Zimbabwe: Primarily Angolan Mopane Woodlands (AT0702), Zambezian and Mopane Woodlands (AT0725), Kalahari Acacia-Baikiaea Woodlands (AT0709).

Bioregions South Africa: Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 3 525 050 km² (gross estimate); AOO much smaller due to dung type and possibly finer-grained soil and woody vegetation specialisation; low population density across a fragmented but widespread range centred on game reserves owing to range contraction of monogastric herbivores, particularly elephant and rhinoceros; some old records lie outside of current reserves, e.g. Christmas Pass, E Zimbabwe; assessed as Least Concern (LC) owing to wide range and protection in various reserves..

Conservation measures: Assessment of conservation status would be improved by quantitative data to support qualitative observations; status probably dependent on continuing protection of elephants, rhinoceros, and woody vegetation within reserves with finer-grained soils; tests of population density in nearby farmland may reveal threats outside of reserves; protected in Hluhluwe–iMfolozi Game Reserve (South Africa) and various national parks: Gorongosa (Mozambique), Etosha (Namibia), Hwange (Zimbabwe), Serengeti (Tanzania).



Onitis setosus

van Lansberge, 1875b

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Benguela' [SW Angola].

Taxonomy: Accepted Group XI species; limited sexual dimorphism (legs), prominence of characters varies with body size.

Distribution: Dry to moist savanna in S central Africa possibly with a W bias: Angola, N Namibia, N Zimbabwe; report from Tanzania requires validation.

Locality data (mean ± SD, range): Average altitude: 1 135 ± 295, 683–1 504 m; average annual rainfall: 417 ± 137, 298–745 mm; average annual temperature (max. + min. /2): 19.2 ± 2.6, 15.0–22.5°C (N=8).

Habitat: No quantitative assessment; limited DBRU collection records from finer-grained soils: sandy clay loam (1), clay (1) in open shrub/woodland (2).

Food types: No quantitative assessment; limited DBRU collection records from dung of large monogastric herbivores: elephant (1), donkey (1).

Temporal activity: Flight activity in darkness during the late summer rainy season (Jan. to Apr.).

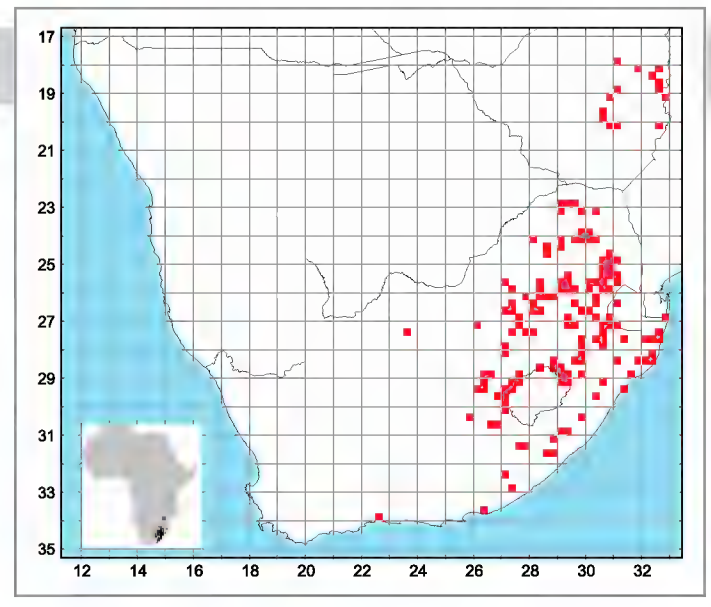
Ecoregions Namibia: N Namibian Savanna Woodlands (AT1316), Angolan Mopane Woodlands (AT0702).

Assessment rationale: EOO = 119 160 km²; AOO possibly smaller according to coincidence of monogastric herbivores with finer-grained soils although quantitative support required for such specialisations; specialisation would, however, account for patchy distribution in Angola, N Namibia and at the moist upper S edge of the Zambezi Valley; assessed as Least Concern (LC) on basis of wide distribution although loss of monogastric herbivores might be detrimental to population density.

Conservation measures: Assessment of conservation status would be improved by quantitative survey data to determine the full EOO and the effect on AOO of ecological associations, particularly those with soil and dung type; protected in Etosha National Park, N Namibia.

Onitis tortuosus

Houston, 1983



No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'ERMELO T[rans]v[aa]l/ (16 km S)' [Mpumalanga, South Africa].

Taxonomy: Accepted Group III species; limited sexual dimorphism (legs), prominence of characters varies with body size.

Distribution: Highlands, E South Africa, E Zimbabwe; coastline, E South Africa, SE Mozambique.

Locality data (mean ± SD, range): Altitude: 1 248 ± 449, 0–2 392 m; annual rainfall: 751 ± 138, 416–1 136 mm; annual temperature (max. + min. /2): 17.0 ± 2.3, 9.9–23.4°C (N=204).

Habitat: Little quantitative data; at Carolina: no clear effect of grassland modification, natural *Themeda* grassland (3), fallow crop field (6), improved Kikuyu pasture (6); DBRU collection records primarily from finer-grained soils: clay (10), sandy clay loam (48), sandy loam (33), sand (8) on pasture/grassland (80) or crop fields (6); few in shrubland (3), open woodland (1), forest (1).

Food types: Little quantitative data; in the Wolkberg: dung type bias to ruminant herbivore dung, cattle (6), rather than omnivore dung, pig (0); DBRU collection records primarily from cattle dung (135); single records from buffalo, rhinoceros and zebra dung;.

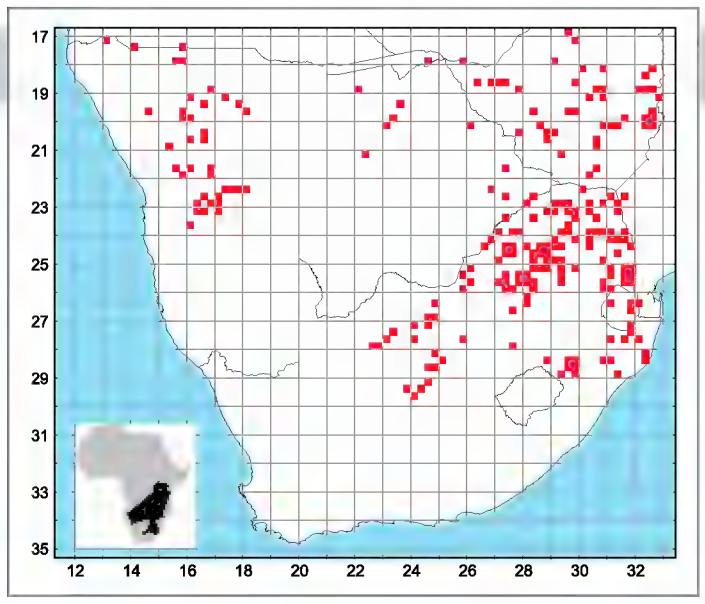
Temporal activity: Diel flight activity in darkness (crepuscular: dusk) (Caveney et al. 1989) during the summer rainy season (Oct. to May) with cool season activity on the warmer coastline (June); attracted to light.

Ecoregions Zimbabwe: Eastern Zimbabwean Montane Forest Grassland Mosaic (AT1006), Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Dry Highveld Grassland (Gh), Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs) (Grassland Biome); Central Bushveld (SVcb) (Savanna Biome) (grassy uplands: Waterberg, Soutpansberg); Indian Ocean Coastal Belt Biome (CB); marginal in three other bioregions.

Assessment rationale: EOO = 348 320 km^2; widespread in dry to moist highland grassland where it is apparently little influenced by pasture improvement and is readily attracted to the dung of cattle; therefore, well-adapted to an agro-ecosytem where transformation varies from: 4–60% (Gh), 6–69% (Gm), and 2–50% (Gs) in South Africa; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by further quantitative data on ecological associations; protected in Abe Bailey, Suikerbosrand and Loskop Dam nature reserves; also Ithala Game Reserve.



Onitis uncinatus

Klug, 1855

= *Onitis fodiens* Boheman, 1857

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. uncinatus*: 'Sena' [central Mozambique]; *O. fodiens*: 'Caffraria tota' [all SE South Africa].

Taxonomy: Accepted Group XVIII species; limited sexual dimorphism (legs), prominence of characters varies with body size.

Distribution: Arid and moist savanna, S to E Africa: N South Africa, Eswatini, N Namibian plateau, N Botswana, Angola, Zimbabwe, Mozambique, Malawi, Tanzania, Kenya; also reported from Democratic Republic of the Congo (DRC), Rwanda, Burundi, Uganda, Ethiopia.

Locality data (mean ± SD, range): Altitude: 1 015 ± 420, 0–1 998 m; annual rainfall: 599 ± 185, 203–1 198 mm; annual temperature (max. + min. /2): 19.8 ± 2.1, 13.7–25.7°C (N=313).

Habitat: In Gauteng bushveld: extreme bias to finer-grained soils, sandy clay loam (138), deep sand (0), in open vegetation, grassland (47), open woodland (73), shaded thickets (18); DBRU collection records largely supportive: clay (14), sandy clay loam (33), sandy loam (56), sand (39) in forest (2), open shrub/woodland (85), pasture/grassland (39).

Food types: At Phalaborwa: strong bias to both ruminant and monogastric herbivore compared to omnivore dung types, cattle (30), elephant (27), pig (2); DBRU collection records supportive: cattle (174), buffalo (6), wildebeest (2), elephant (8), rhinoceros (3), zebra (2), horse (1), donkey (1).

Temporal activity: Diel flight activity in darkness (crepuscular: dusk/dawn and nocturnal) (Caveney et al. 1989) in the summer rainy season (Oct. to Apr.); in Gauteng bushveld: early summer peak (Nov. to Jan.) tailing off into late summer (Feb. to Apr.); attracted to light.

Ecoregions Namibia, Botswana, Zimbabwe: In the E: Southern African Bushveld (AT0717), Zambezian and Mopane Woodlands (AT0725), Southern Miombo Woodlands (AT0719); in the W: Angolan Mopane Woodlands (AT0726), N Namibian Savanna Woodlands (AT1316), N Kalahari Xeric Woodlands (AT1309).

Bioregions South Africa: Eastern Kalahari Bushveld (SVk), Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome); also N Sub-Escarpment Grassland (Gs) (Grassland Biome); margins of four other bioregions.

Assessment rationale: EOO = 4 665 140 km^2 (gross estimate); AOO reduced by soil type bias; in southern Africa, centred on the finer-grained soils of the E and W savanna regions separated by the deep sands of the southern Kalahari basin; extremely widespread; also readily colonises cattle dung in open vegetation on farms; assessed as Least Concern (LC).

Conservation measures: None required; widely distributed in farmland, national parks and game reserves; protected in the Kruger NP (South Africa), Lake Mutirikwe GR (Zimbabwe), Gorongosa NP (Mozambique), Etosha NP (Namibia), Manyara NP (Tanzania), Masai Mara GR (Kenya).

Onitis viridulus

Boheman, 1857

= *Onitis consanguineus*, Felsche, 1911
= *Onitis insulanus*, Kolbe, 1914
= *Onitis viridulus* Boheman, 1857, var. *laevissimus* Gillet, 1911 (*pars*)

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. viridulus*: 'Caffraria tota' [all SE South Africa]; *O. consanguineus*: 'Harrar' [Ethiopia]; *O. insulanus*: 'Insel Wau im Kivu-See (Ruanda)' [Wau Island, Lake Kivu, Rwanda]; var. *laevissimus*: 'd'Afrique orientale anglaise (Naivasha, Rift Valley);.....d'Abyssinie' [Kenya, Ethiopia].

Taxonomy: Accepted Group III species; limited sexual dimorphism (legs), prominence of characters varies with body size.

Distribution: S to NE African savanna; N South Africa, Eswatini, NE Namibia, N Botswana, Angola, Zimbabwe, Mozambique, Malawi, Rwanda, Tanzania, Kenya, Ethiopia; also reported from Democratic Republic of the Congo (DRC), Burundi, Uganda; report from S Arabia requires validation; Gambia record presumably an error.

Locality data (mean ± SD, range): Altitude: 803 ± 517, 0–1 958 m; annual rainfall: 715 ± 167, 377–1 275 mm; annual temperature (max. + min. /2): 20.2 ± 2.2, 14.3–25.2°C (N=206).

Habitat: In Gauteng bushveld: bias to finer-grained soils, sandy clay loam (27), deep sand (7) in various vegetation types, grassland (12), open woodland (7), shaded thicket (15); supported by DBRU collection records: clay (18), sandy clay loam (25), sandy loam (28), sand (23) on pasture/grassland (39), open shrub/woodland (43), thicket/forest (7).

Food types: No quantitative assessment; DBRU collection records from various ruminant and monogastric dung types: cattle (93), buffalo (4), wildebeest (1), elephant (26), hooked-lipped (black) (1) and square-lipped (white) (5) rhinoceros, hippopotamus (1), warthog (1), zebra (2), horse (1).

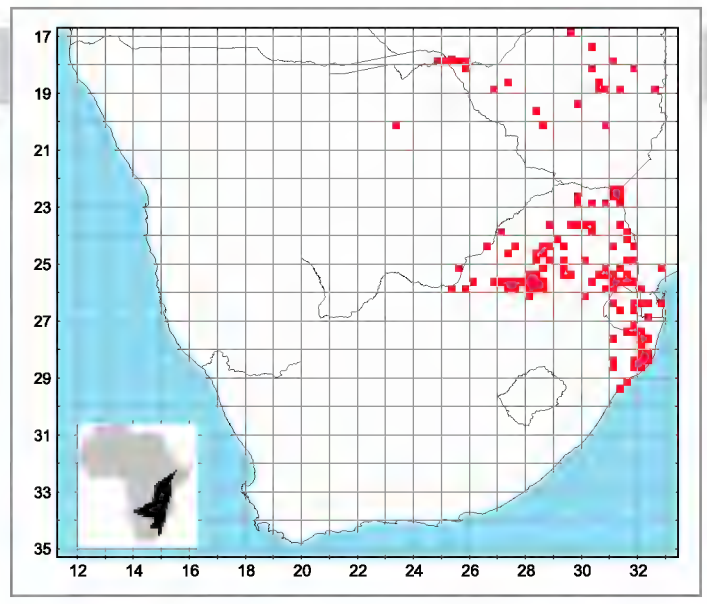
Temporal activity: Diel flight activity in darkness (crepuscular: dusk/dawn) (Caveney et al. 1989) in the summer rainy season (Oct. to May); also in the cooler season at the warmer coastline (June to Aug.); bias to colonisation of older dung (0–2 day old, 34%; 2–4 day, 53%; n=66); attracted to light.

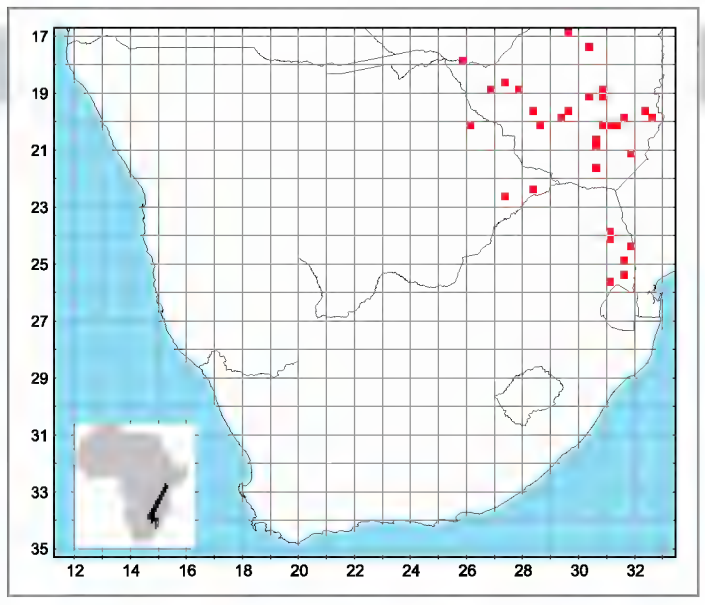
Ecoregions Botswana, Zimbabwe, Mozambique: Zambezian Baikiaea Woodlands (AT0726), Southern African Bushveld (AT0717), Zambezian and Mopane Woodlands (AT0725), Southern Miombo Woodlands (AT0719), Maputaland Coastal Forest Mosaic (AT0119), margins of two other ecoregions.

Bioregions South Africa: Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome); also Mopane (SVmp) (Savanna Biome), N Indian Ocean Coastal Belt Biome (CB); marginal in three other bioregions.

Assessment rationale: EOO = 4 084 025 km² (gross estimate); AOO would probably be more restricted due soil type specialisation; however, extremely widespread on finer-grained soils in both savanna reserves and farmland owing to generalist vegetation and dung type associations; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by further quantitative data on ecological associations, particularly food associations; protected in many national parks and game reserves: Kruger, Hluhluwe–iMfolozi (South Africa), Gorongosa (Mozambique), Bicuar (Angola), Manyara (Tanzania).





Onitis westermanni

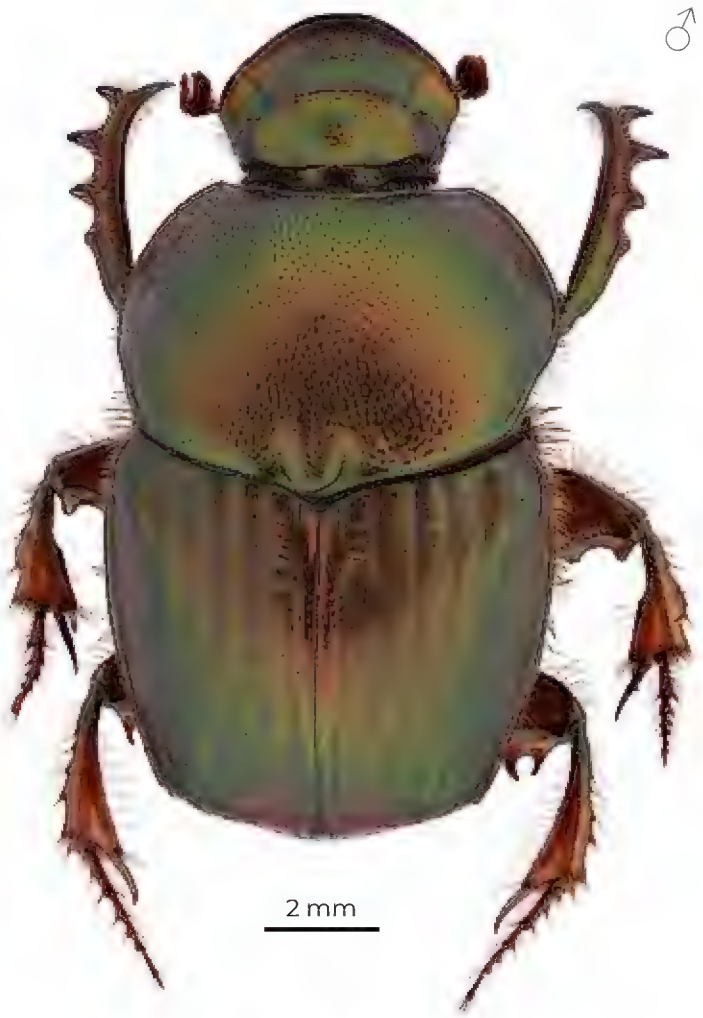
van Lansberge, 1886

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

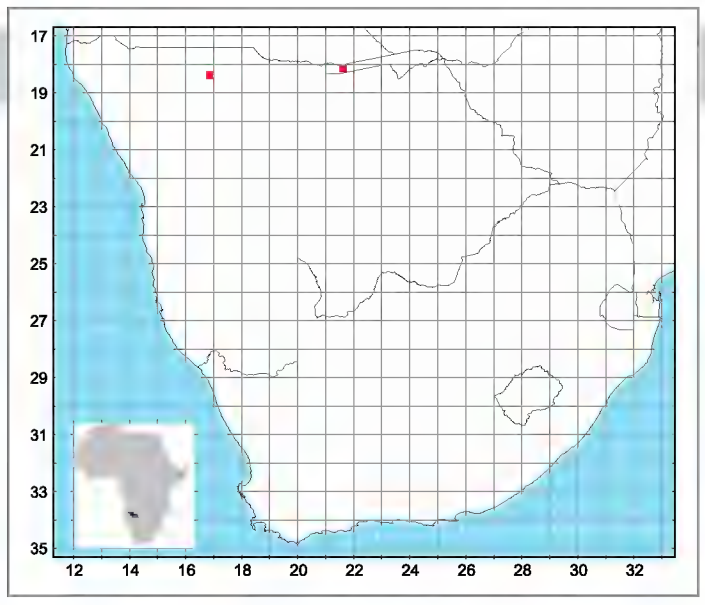
Type locality: 'Zambèze', lectotype 'Zambesi' [inexact, southern Africa].
Taxonomy: Accepted Group XVII species; limited sexual dimorphism (legs), prominence of characters varies with body size.
Distribution: SE and E African savanna: NE South Africa, NE Botswana, Zimbabwe, Zambia, Tanzania, Kenya; reports from Ethiopia, Namibia require validation.
Locality data (mean ± SD, range): Altitude: 954 ± 378, 268–1 521 m; annual rainfall: 655 ± 129, 333–1 021 mm; annual temperature (max. + min. /2): 20.5 ± 1.8, 16.9–25.6°C (N=48).
Habitat: No quantitative assessment; DBRU collection records on sandy clay loam (9), sandy loam (7), and sand (5) in pasture/grassland (8), open woodland (7), and fallow crop field (1).
Food types: No quantitative assessment; DBRU collection records primarily on cattle dung (31); also buffalo (2), elephant (1), hooked-lipped (black) (1) and square-lipped (white) (1) rhinoceros and human dung (1).
Temporal activity: Diel flight activity in darkness (crepuscular: dusk) (Caveney et al. 1989) in the summer rainy season (Nov. to Apr.); attracted to light.
Ecoregions Botswana, Zimbabwe: Southern Miombo Woodlands (AT0719); also moister areas Southern African Bushveld (AT0717), Zambezian and Mopane Woodlands (AT0725); marginal in two other ecoregions.
Bioregions South Africa: Moister, warmer areas Lowveld (SVl) (Savanna Biome).
Assessment rationale: EOO = 944 160 km^2 (gross estimate); no quantitative data on ecological associations, but widespread and recorded equally in woodland and grassland, primarily on finer-grained soils, with many records from cattle dung in farmland; in South Africa, primarily restricted to a protected area in the NE lowlands; assessed as Least Concern (LC).
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; protected in Kruger National Park (South Africa), Lake Mutirikwe Game Reserve (Zimbabwe), Meru National Reserve (Kenya).



Genus *Platyonitis* Janssens, 1942

Type species and designation: *Platyonitis oberthuri* Janssens, 1942, by monotypy.
Synonyms: = *Epionitis* Balthasar, 1942: Type species: *Epionitis tarsatus* Balthasar, 1942, by monotypy.
Last review: Genus created by Janssens (1942); valid new species added by Krikken, (1974) and Ferreira (1976b, plus key).

Platyonitis Janssens, 1942, is currently represented by three Afrotropical species found in moist savanna of SW Angola plus N Namibia (1) with a disjunction to moist or dry savanna of E Africa (Kenya, N Tanzania) (2). Mozambique record likely an error due to a mislabeled specimen (Bezděk & Sladecek 2012). All species are apparently associated with elephant dung, which is why the single species in SW Africa is assessed as Vulnerable (VU) since its range in N Namibia remains unprotected and that in Angola was subject to decimation of elephant populations.



Platyonitis bicuariensis

Ferreira, 1976b

No synonyms

Global: VU (see IUCN Red List – VU)

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Angola: no° 1674 Bicuari N.P. (Nr. Camp)' [Bicuar National Park, Angola].

Taxonomy: Accepted species; limited sexual dimorphism (legs).

Distribution: Deep sands in open woodland; SE Angola and Ovamboland, N Namibia.

Locality data (mean ± SD, range): Altitude: 1 092 ± 129, 952–1 207 m; annual rainfall: 609 ± 180, 473–813 mm; annual temperature (max. + min. /2): 22.2 ± 0.8, 21.4–23.0°C (N=3).

Habitat: No quantitative assessment; DBRU collection records on sand (1), sandy loam (1) in shrub/woodland (1), riverine grassland (1).

Food types: No quantitative assessment; DBRU collection records only from monogastric herbivore (elephant) dung (2).

Temporal activity: Flight activity during darkness in the summer rainy season (Dec.).

Ecoregions Namibia: Angolan Mopane Woodlands (AT0702), Zambezian Baikiaea Woodlands (AT0726).

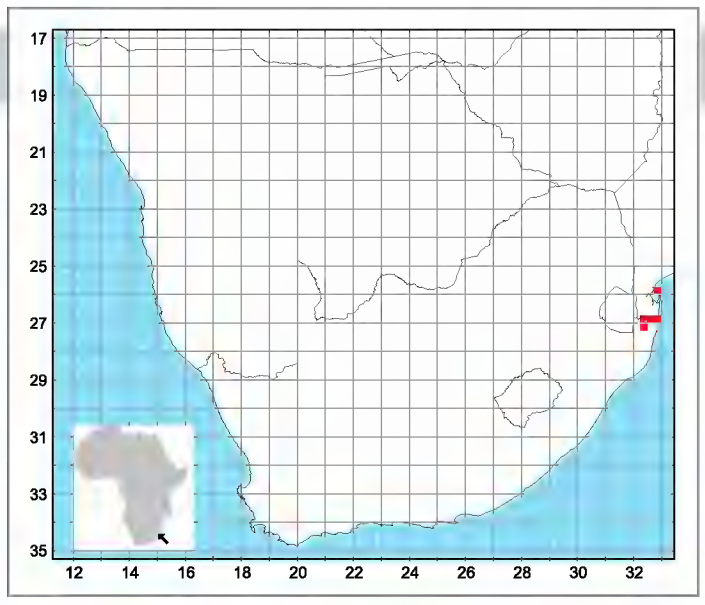
Assessment rationale: EOO = 88 760 km^2; probably a soil and dung type specialist as the type series of 14 specimens were all taken from deep sands on elephant dung in 1974; however, the meagre collection data are inconclusive; in 2007, following decimation of elephant populations during the Angolan civil war, the occurrence of elephants around the type locality was assessed only as 'possible' by the IUCN although news reports from 2013 indicate that elephants have returned; in view of recent range contraction and fragmentation history for elephants in both Namibia and Angola, the conservation status of *P. bicuariensis* is currently assessed as Vulnerable (VU), since, despite a large EOO, it is known from only three localities.

Conservation measures: To determine its conservation status more precisely, a quantitative survey is required to accurately assess its EOO, AOO, ecological associations and population density; particular attention needs to be paid to (1) the impact of possible temporary disappearance of elephants from around the type locality in Bicuar National Park and other parts of SE Angola and (2) the effects of interaction with humans resulting in only possible or occasional elephant occurrence in parts of Ovamboland where *P. bicuariensis* has been recorded.

Genus *Tropidonitis* Janssens, 1937

Type species and designation: *Onitis paradoxus* Boheman, 1857, by subsequent designation (Janssens 1937).
Synonyms: None.
Last review: Genus created and reviewed by Janssens (1937).

Tropidonitis Janssens, 1937, is a monotypic genus associated with elephant dung showing a small EOO on coastal sands in SE Africa where it is known only from the Maputaland Centre of Endemism. Although recently recorded from protected parts of this range, it is assessed as Vulnerable (VU).



Tropidonitis paradoxus

(Boheman, 1857)

No synonyms

Global: VU

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Onitis paradoxus*: 'Caffraria' [SE South Africa].
Taxonomy: Accepted species; limited sexual dimorphism (legs).
Distribution: Past and present records all from the coastal Maputaland Centre of Endemism, SE Mozambique and NE KwaZulu-Natal, South Africa.
Locality data (mean ± SD, range): Altitude: 36 ± 21, 0–60 m; annual rainfall: 720 ± 64, 654–808 mm; annual temperature (max. + min. /2): 22.5 ± 0.1, 22.3–22.6°C (N=6).
Habitat: No quantitative assessment; occurs in an area of wooded deep sands; one DBRU collection record in shrubland.
Food types: No quantitative assessment; one DBRU collection record on elephant dung; in extensive sampling: not recorded in Maputo Elephant Reserve using pig dung as bait, only one recorded in Sand Forest in Sileza Nature Reserve using elephant dung as bait.
Temporal activity: Unknown; probably active in darkness in the summer rainy season (Nov. to Feb.).
Ecoregions Mozambique: Maputaland Coastal Forest Mosaic (AT0119).
Bioregions South Africa: Straddling the edge of the Lowland (SVl) Bioregion (Savanna Biome) and the N of the Indian Ocean Coastal Belt Biome (CB).
Assessment rationale: EOO = 2 455 km^2; noted as rare by the species author (Boheman 1857); possibly always restricted to the Maputaland Centre of Endemism owing to specialised habitat (deep sand, woodland) and dung type associations (monogastric herbivore, especially elephant); occupies a small range, so qualifies for Vulnerable (VU) (EOO < 20 000 km^2 and < 10 locations) or even Endangered (EN) status (EOO < 5 000 km^2 and < 5 locations).
Conservation measures: To determine its conservation status more precisely a quantitative survey is required to accurately assess its EOO, AOO, ecological associations and population density; it is probable that continuing protection of woodland and elephants on deep sands in Tembe Elephant Park are essential to conserve this species.

TRIBE ONTHOPHAGINI

Burmeister, 1846

As Onthophagidae; Type genus: *Onthophagus* Latreille, 1802.

Synonyms:

Alloscelides Janssens, 1946; Type genus *Alloscelus* Boucomont, 1923b.

Whereas morphological phylogeny indicates monophyly for the tribe Onthophagini (Philips 2016), molecular phylogeny suggests paraphyly (Monaghan et al. 2007). The tribe currently comprises 37 genera although others are being added, primarily by separating species groups from the largest genus, *Onthophagus* Latreille, 1802, and raising them to generic level. Many genera are endemic to the Afrotropical (24) or Oriental regions (4). Several are shared between the **(A)** Afrotropical and Palaearctic regions (*Euonthophagus* Balthasar, 1959); **(B)** Afrotropical and Oriental (*Digitonthophagus* Balthasar, 1959; *Haroldius* Boucomont, 1914); **(C)** Oriental and Palaearctic (1); or, the **(D)** Afrotropical, Oriental and Palaearctic or S Palaearctic (*Caccobius* Thomson, 1859; *Cleptocaccobius* Cambefort, 1984; *Phalops* Erichson, 1847b; *Proagoderus* van Lansberge, 1883); whereas one, **(E)** *Onthophagus s. str.* Latreille, 1802, is found globally in warmer regions of the Afrotropical, Oriental, Palaearctic, Australasian, Nearctic and Neotropical regions including Madagascar.

Many of the endemic genera (at least 19) and one Afrotropical/Oriental genus are suspected to be ant- or termite-associated although evidence is limited. Genera with such putative habits mostly occupy terminal positions on partial morphological phylogenies (Philips 2016). The remainder mainly comprise tunnelling genera although at least three comprise or include kleptocoprid species.

A total of 16 onthophagine genera are recorded from South Africa, Botswana and Namibia as of November 2017, although two others have since been added (see Preamble, Dierkens et al. (2017), Roggero et al. (2019)). Below, genera are ranked from most basal to most derived according to the morphological phylogeny of Philips (2016) with the further insertion of one recently described genus. They reflect the behavioural patterns shown by the entire tribe. Most are probably dominated by tunnelling habits (10: one with some kleptocoprid species). The more terminally derived remainder are probably dominated by kleptocoprid (2) or ant or termite associations (4: one with no species accounts prepared).

In South Africa, Botswana and Namibia (Nov. 2017):

(1) *Proagoderus* van Lansberge, 1883: Represented by 15 tunnelling species centred on savanna (12), upland grassland (2) or Kalahari deep sands (1) with six specialised on monogastric herbivore dung, four with distributions extending into the E tropics.

(2) *Digitonthophagus* Balthasar, 1959: Represented by three tunnelling species centred on savanna (1) or SW Arid climate (2).

(3) *Phalops* Erichson, 1847b: Represented by 13 tunnelling species centred on savanna (9), Kalahari deep sands (1) or variously across savanna, upland grassland and Karoo (3).

(4) *Kurtops* Roggero, Barbero & Palestrini, 2016: Represented by three species with distributions centred on Kalahari sands (2) or unknown range (1).

(5) *Onthophagus s. str.* Latreille, 1802: Represented by aproximately 120 named, but not necessarily validated, tunnelling and kleptocoprid species with a large, but unknown number of additional unnamed species; 82 species in 78 accounts show large or small ranges centred on savanna (47), upland grassland (16), savanna and upland grassland (1), Kalahari deep sands (5), Upper Karoo (3), SW Arid late summer rainfall region (6), E forest (1), or winter and bimodal rainfall regions (7).

(6) *Hamonthophagus* Roggero, Dierkens, Barbero & Palestrini, 2016: Represented by three species distributed in the SW Arid late summer rainfall region (1) or savanna (2).

(7) *Euonthophagus* Balthasar, 1959: Represented by nine species for which only four names could be validated with distributions centred on savanna (2), Kalahari deep sands (1) and Upper Karoo (1); one a monogastric dung specialist.

(8) *Hyalonthophagus* Palestrini & Giacone, 1988: Represented by two species centred on savanna (1) or Kalahari deep sands (1).

(9) *Milichus* Péringuey, 1901: Represented by two species, of which only one named savanna monogastric dung specialist could be validated.

(10) *Caccobius* Thomson, 1859: Represented by over 20 possibly kleptocoprid species; habits mostly based on small body size; names could be validated for only six species, mostly centred on savanna (5) or upland grassland (1).

(11) *Mimonthophagus* Balthasar, 1963b: Represented by only three savanna species; one a monogastric dung specialist.

(12) *Cleptocaccobius* Cambefort, 1984: Represented by ± six kleptocoprid species, for which names could be validated for only three savanna taxa.

(13) *Haroldius* Boucomont, 1914: Represented by a single ant-associated species from savanna; in the recent partial revision of tribal classification (Tarasov & Dimitrov 2016), this genus was classified with 'Basal Scarabaeinae' on molecular grounds not in the Onthophagini on morphological grounds (Philips 2016).

(14) *Caccobiomorphus* Balthasar, 1964b: Monotypic, associated with ponerine ants in savanna and, possibly, also forest in the tropics.

(15) *Heteroclitopus* Péringuey, 1901: Represented by a single, possibly termite-associated species in savanna.

Onthophagine genera show a strong bias to greater diversity in savanna. Few onthophagine species are regarded as threatened.

Genus *Caccobiomorphus* Balthasar, 1964b

Type species and designation: *Caccobiomorphus brevisetosus* Balthasar, 1964b, by original designation.
Synonyms: = *Megaponerophilus* Ferreira, 1972: Type species: *Caccobius megaponerae* Brauns, 1914, by original designation.
Last review: Reviewed as *Megaponerophilus* Janssens, 1949, by Cambefort (1979).

According to Branco (2011), rules of nomenclature cause the authorship of the earlier generic name, *Megaponerophilus* Janssens, 1949 (name only), to shift to Ferreira, 1972 (first description). This reduces *Megaponerophilus* Ferreira, 1972, to a synonym as it would post-date the description of *Caccobiomorphus* Balthasar, 1964b. The small-bodied genus, *Caccobiomorphus*, is now monotypic as species described from different localities under various different names are considered to be synonyms that are associated with the same widespread species of predatory ant.

Caccobiomorphus megaponerae

(Brauns, 1914)

= *Caccobiomorphus brevisetosus* Balthasar, 1964b
= *Caccobiomorphus congolanus* Balthasar, 1964b

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Caccobius* (*Caccophilus*) *megaponerae*: 'Bulawayo, S. Rhodesia' [Bulawayo, Zimbabwe]; *C. brevisetosus*: 'Ostafrika, Mons Martii' [untraced locality, East Africa]; *C. congolanus*: 'Congo, in der Umgebung von Stanleyville' [environs of Kisangani, Democratic Republic of the Congo (DRC)].

Taxonomy: Accepted species; limited sexual dimorphism (head, prothoracic disc).

Distribution: Centred in lower-altitude savanna, SE Africa: South Africa, Zimbabwe, Zambia, Mozambique; one synonym in tropical forest area of Central Africa: Democratic Republic of the Congo (DRC).

Locality data (mean ± SD, range): Altitude: 703 ± 502, 76–1 388 m; annual rainfall: 600 ± 187, 391–961 mm; annual temperature (max. + min. /2): 22.1 ± 2.5, 18.7–23.6°C (N=7).

Habitat: No quantitative assessment; holotype recorded from a nest of the predatory, termitophagous ponerine ant, *Megaponera analis* (Latreille, 1802) that is widespread in dry to moist savanna and dry forest of sub-Saharan Africa; also seen moving in columns of ponerine ants.

Food types: No quantitative assessment; cited as possibly feeding on the termite prey of *Megaponera* brought into the nests.

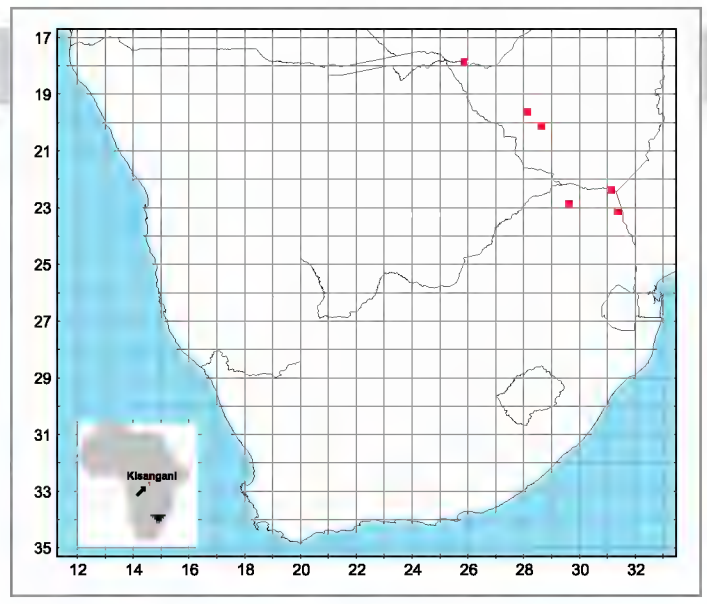
Temporal activity: Diurnal ambulatory activity in ant columns during the summer rainy season (Dec. to May).

Ecoregions Zimbabwe: Zambezian and Mopane Woodlands (AT0725), Southern African Bushveld (AT0717), Zambezian Baikiaea Woodlands (AT0726).

Bioregions South Africa: Mopane (SVmp) (Savanna Biome).

Assessment rationale: EOO = 299 670 km² (southern Africa only; underestimated); putative range extends from dry savanna to rainforest at Kisangani; synonymy of *C. congolanus* supported by records of *Megaponera* host from forest localities in Cameroon; rarity in collections related to infrequent discovery due to highly specialised habits; assessed as Least Concern (LC) on basis of large range.

Conservation measures: Conservation status is linked to that of its *Megaponera* host, which is not considered at risk although the tropical dry forest part of its range is fragmented; assessment of status would be improved by further distributional and quantitative ecological data; protected in Kruger National Park (South Africa).



Genus *Caccobius* Thomson, 1859

Type species and designation: *Scarabaeus schreberi* Linnaeus, 1767, by original designation.
Synonyms: = *Histeridium* Motschulsky, 1860: Type species: *Scarabaeus schreberi* Linnaeus, 1767, by monotypy.

Subgenera:

***Caccobius s. str.* Thomson, 1859:** Type species: *Scarabaeus schreberi* Linnaeus, 1767, by original designation.
***Cacconemus* Jekel, 1872:** Type species: *Onthophagus castaneus* Klug, 1855, by subsequent designation (Branco 2011).
***Caccophilus* Jekel, 1872:** Type species: *Caccophilus himalayanus* Jekel, 1872, by subequent designation (Cambefort 1979: Group V).

Last review: Genus divided into 12 species groups by Cambefort (1979); Group IV = subgenus, *Tomogonus* d'Orbigny, 1902, now raised to generic status; Group XI now transferred to genus, *Cleptocaccobius* Cambefort, 1984; Group XII = *Caccobiomorphus* Balthasar, 1964b; new Afrotropical *Caccobius* species added after 1979 by Cambefort (1980, 1984), Walter (2014).

The long-established genus, *Caccobius* Thomson, 1859, currently comprises 103 small-bodied species in the Afrotropical (58), Oriental (30) and Palaearctic regions (15). These species are currently classified within three subgenera (*Caccobius s. str.*; *Cacconemus* Jekel, 1872; *Caccophilus* Jekel, 1872). They are also classified into nine groups (Cambefort 1979) after removal of three further groups into other genera. Cambefort's Group I is cited as *Caccobius s. str.* (Palaearctic/Oriental) and his Group III as *Cacconemus* (currently, two Afrotropical species). However, membership of *Caccophilus*, as defined from 10 species by Jekel (1872), is spread across four different groups (V (Oriental), VIII (Palaearctic/Oriental), IX (Afrotropical/Oriental), X (Afrotropical). Furthermore, the three remaining groups (Cambefort 1979) are also classified as *Caccophilus*: Group II (Palaearctic/Oriental), VI (two E African species), VII (one W African species).

Species pages are presented for only six *Caccobius* species classified in four different groups. They represent just a small proportion of the *Caccobius* species recognised in collections from South Africa, Botswana and Namibia. Of five species described from South Africa, only three could be matched to reference material. However, a further three species described from elsewhere were more-or-less validated as also occurring in southern Africa. Even though > 15 other *Caccobius* species were recognised in collections from South Africa, Botswana and Namibia (mainly from South Africa), none could be matched to described species with confidence. Some are probably undescribed.

The six species for which species pages are provided are all widespread, either along the E seaboard (four) or across Africa (two) (Group III (1), Group VI (1), Group IX (2), Group X (2)).

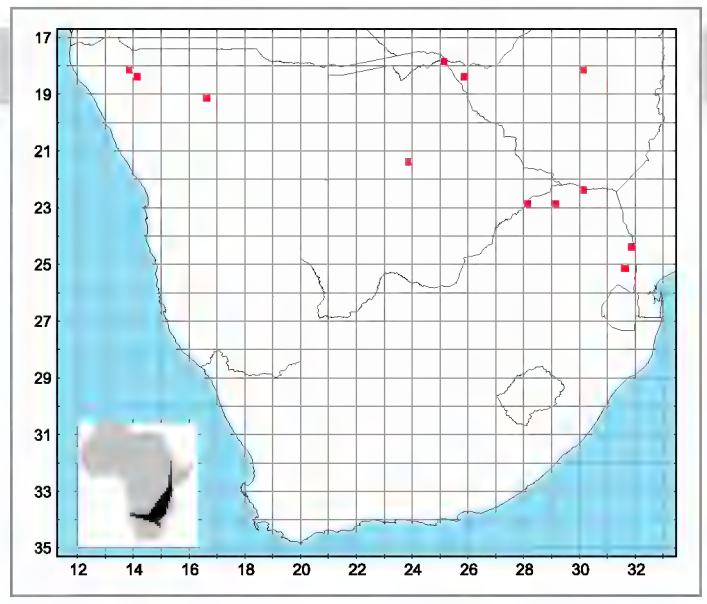
Caccobius castaneus

(Klug, 1855)

= *Caccobius medioniger* Ancey, 1883

Global: DD

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: As *Onthophagus castaneus* 'Sena' [central Mozambique]; *C. medioniger*: 'Abyssinie' [inexact: Ethiopia].

Taxonomy: Accepted Group III species in subgenus, *Cacconemus* Jekel, 1872; species cited, here, as *C. castaneus* requires validation in comparison to *Caccobius (Cacconemus) pseudolaevis* d'Orbigny, 1908.

Distribution: Dry to moist savanna woodlands from S to E to NE Africa; South Africa, Botswana, Namibia, Mozambique, Zimbabwe, Kenya; also cited from Eritrea, Ethiopia; citation from Chad may represent a close relative, *Caccobius (Cacconemus) pseudolaevis*, described from Chad.

Locality data (mean ± SD, range): Altitude: 863 ± 390, 286–1 530 m; annual rainfall: 494 ± 158, 305–754 mm; annual temperature (max. + min. /2): 21.2 ± 2.2, 16.3–23.4°C (N=12).

Habitat: No quantitative assessment; recorded on clay, sandy loam and sand at localities in Kenya; no recorded vegetation data.

Food types: No quantitative assessment; recorded on cattle, buffalo and elephant dung at localities in Kenya.

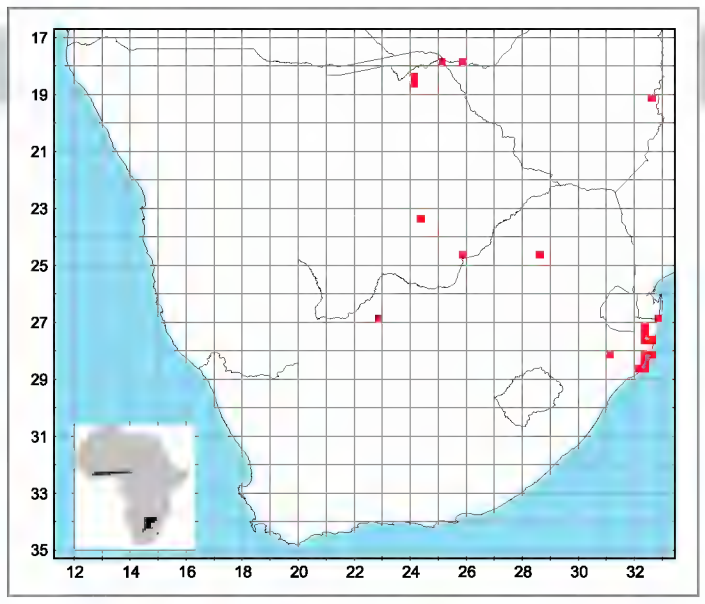
Temporal activity: Diel flight periodicity unknown; recorded during the summer rainy season (Nov. to Feb.).

Ecoregions Namibia, Botswana, Zimbabwe: Southern Miombo Woodlands (AT0719), Zambezian and Mopane Woodlands (AT0725), Kalahari Acacia-Baikiaea Woodlands (AT0709), Angolan Mopane Woodland (AT0702), Namibian Savanna Woodlands (AT1316).

Bioregions South Africa: N Central Bushveld (SVcb), Mopane (SVmp), N Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 2 314 560 km²; only recorded sporadically in low numbers, but over a wide range; poorly known ecologically with validation of taxonomic identity required; thus, assessed as Data Deficient (DD).

Conservation measures: Assessment of conservation status would benefit from validation of differences between *C. castaneus* and *C. pseudolaevis*; quantitative data on ecological associations is also required to generate an assessment; protected in various reserves, including Kruger National Park (South Africa), Etosha National Park (Namibia), Meru National Reserve (Kenya).



Caccobius cavatus

d'Orbigny, 1908

No synonyms

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'Sud du lac Tchad: mont des Niellims sur le moyen Chari...,Kiao-Kala sur les rives de moyen Chari..., Rhodesia: Salisbury' [mid-reaches, Chari River, Chad; Harare, Zimbabwe].

Taxonomy: Accepted Group X species in subgenus, *Caccophilus* Jekel, 1872; sexual dimorphism (head, prothoracic disc); prominence of characters varies with body size.

Distribution: Widespread on deep sands across dry to moist savanna of W and southern Africa: South Africa, Zimbabwe, Botswana, NE Namibia, Chad, Côte d'Ivoire; scattered records presumably a collection artefact related to small body size; disjunction between W and S Africa may also be a collection artefact.

Locality data (mean ± SD, range): Altitude: 539 ± 477, 0–1 065 m; annual rainfall: 693 ± 202, 320–1 006 mm; annual temperature (max. + min. /2): 21.4 ± 1.2, 17.9–23.0°C (N=26).

Habitat: In Botswana: strong bias to moister NE (3 615) compared to arid SW (202); in uMkhuze Game Reserve: extreme bias to deep sand (5.5) compared to sand on clay (0.4), sandy clay loam (0.0), clay (0.0) with 70% of abundance in grassland (cited as *Caccobius* sp. 5); limited DBRU collection records on sand (2) in grassland (1), shrubland (1), forest/thicket (2).

Food types: In Botswana: mainly sampled to dung (pig: 895; elephant: 592; cattle: 521; sheep: 1 795), few to carrion (chicken livers: 14); in Côte d'Ivoire: similar bias to human dung (133) compared to that of cattle (58); limited DBRU collection records on cattle dung (2).

Temporal activity: Flight activity in darkness during the summer rainy season (Oct. to Mar.).

Ecoregions Botswana, Zimbabwe: Kalahari Xeric Savanna (AT1309), Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian Baikiaea Woodlands (AT0726), Zambezian and Mopane Woodlands (AT0725), Southern Miombo Woodlands (AT0719).

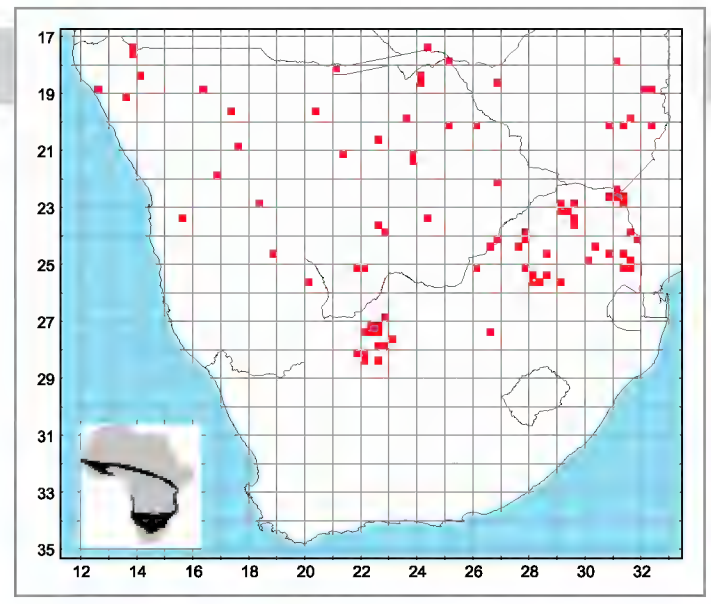
Bioregions South Africa: Eastern Kalahari Bushveld (SVk), Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome); Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 861 245 km^2 (gross estimate); AOO would be somewhat smaller owing to soil specialisation although sandy soils are widespread across its range; locally abundant and attracted to a range of dung types, but data on vegetation associations insufficient to determine effects of habitat transformation; assessed as Least Concern (LC) on basis of wide range and generalist dung association.

Conservation measures: Assessment of conservation status would be improved by quantitative data on vegetation associations and possible effects of habitat transformation; protected in Chobe National Park (Botswana), uMkhuze Game Reserve (South Africa).

Caccobius ferrugineus

(Fahraeus, 1857)



No synonyms

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Onthophagus ferrugineus*: 'prope fluvium Limpopo' [near Limpopo River, southern Africa].

Taxonomy: Accepted Group IX species in subgenus, *Caccophilus* Jekel, 1872; sexual dimorphism (prothoracic disc), characters vary with body size.

Distribution: Widespread in warm, dry to moist, sandy savanna from S to E to W Africa: South Africa, Mozambique, Zimbabwe, Botswana, Namibia, Angola, Zambia, Kenya, Côte d'Ivoire; also reported from Malawi, Tanzania, Democratic Republic of the Congo (DRC), Somalia, Gabon, Nigeria, Benin, Senegal.

Locality data (mean ± SD, range): Altitude: 951 ± 337, 0–1 850 m; annual rainfall: 510 ± 198, 85–1 254 mm; annual temperature (max. + min. /2): 20.4 ± 1.9, 13.4–24.6°C (N=137).

Habitat: In Gauteng bushveld: strong bias to deep sand (363) compared to sandy clay loam (8) and to grassland (265) compared to open woodland (61) or shaded thicket (45); on deep sand in Botswana: extreme bias to moister NE (4 425) compared to arid SW (79); partly supported by DBRU collection records on sand (17), sandy loam (3), sandy clay loam (1) in grassland (8), shrubland (3), open woodland (10), fallow crop field (1).

Food types: On deep sand in Botswana: bias to dung of omnivores (pig, 2 033), less on dung of monogastric herbivores (elephant, 1 211) and ruminant herbivores (cattle, 385; sheep, 853), rare on carrion (chicken livers, 22); similar on sandy loam at Phalaborwa: dung of pig (559), elephant (110), cattle (74); DBRU collection records reflect commonly sampled dung types: cattle (20), wildebeest (1), elephant (4), zebra (1), human/cattle or buffalo mix (2).

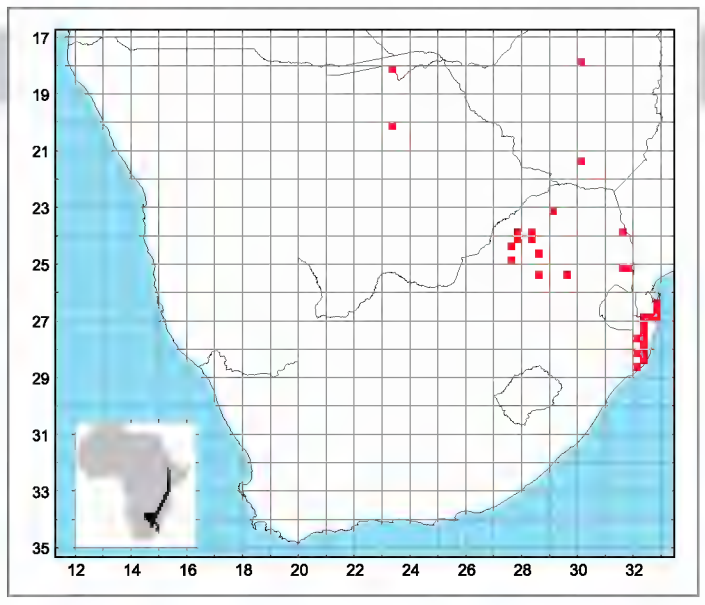
Temporal activity: Flight activity during darkness in the summer rainy season (Oct. to Apr.); in Gauteng: flies from Oct. to Feb. at 18:00–20:00 in cooler months (Nov., Feb.) and 18:00–22:00 in warmer mid-summer (Jan.); at Phalaborwa: equally abundant in warm weather after light (256) or heavy rain (210), or in hot, dry weather (266); attracted to light.

Ecoregions Namibia, Botswana, Zimbabwe: Kalahari Xeric Savanna (AT1309), Namibian Savanna Woodlands (AT1316), but more abundant in Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian Baikiaea Woodlands (AT0726), Zambezian and Mopane Woodlands (AT0725), Southern African Bushveld (AT0717), Southern Miombo Woodlands (AT0719); marginal in two other ecoregions.

Bioregions South Africa: Mostly, W Eastern Kalahari Bushveld (SVk), Central Bushveld (SVcb), Mopane (SVmp), N Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 4 823 540 km² (gross estimate); AOO would be limited by soil type bias although sandy soils are widespread across its very large range; association with open vegetation would be an advantage as clearance of woodland would presumably not be detrimental to population density; despite a bias to omnivore dung, found in abundance on various dung types in both farmland and reserves; assessed as Least Concern (LC).

Conservation measures: None recommended; protected in various national parks including Kruger (South Africa), Chobe (Botswana).



Caccobius histerinus

(Fahraeus, 1857)

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Onthophagus histerinus*: 'juxta fluvium Gariep' [probably inaccurate; near Orange River, South Africa].

Taxonomy: Accepted Group VI species in subgenus, *Caccophilus* Jekel, 1872; material cited here as *C. histerinus* requires validation; however, it is assumed to be identified correctly as it is uniformly similar in length to the type (4.5 mm) whereas a very close, South African relative is uniformly smaller (± 3 mm); also needs to be compared with *C. longipennis* d'Orbigny, 1904 (type: 4.3 mm long), described from 'Abyssinie: environs de Diré Daoua' [Dire Dawa, Ethiopia], but range cited as far S as Zambia; minor sexual dimorphism (head).

Distribution: Mainly lowland, sandy savanna; possibly patchily distributed along the entire E seaboard from S to NE Africa: South Africa, NE Namibia, N Botswana, Zimbabwe, Mozambique; also cited from Democratic Republic of the Congo (DRC), Malawi, Tanzania, Kenya, Eritrea.

Locality data (mean ± SD, range): Altitude: 474 ± 525, 0–1 503 m; annual rainfall: 696 ± 148, 436–1 006 mm; annual temperature (max. + min. /2): 21.3 ± 1.5, 18.3–23.1°C (N=38).

Habitat: In uMkhuze Game Reserve: extreme bias to deep sand (4.1) compared to sand over clay, sandy clay loam, clay (all: 0) (cited as *Caccobius* sp. 4); small, very close relative found on sandy clay loam (0.1) and clay (0.2) (cited as *Caccobius* sp. 7); no adequate quantitative assessment on vegetation associations: found in low numbers in both forest and grassland on deep sands of Maputo Special Reserve.

Food types: No quantitative assessment; no data.

Temporal activity: Diel flight periodicity unknown; seasonal activity in the summer rainy season (Nov. to Feb.).

Ecoregions Botswana, Zimbabwe, Mozambique: Zambezian and Mopane Woodlands (AT0725), Southern Miombo Woodlands (AT0719), Southern African Bushveld (AT0717), Maputaland Coastal Forest Mosaic (AT0119).

Bioregions South Africa: Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome); N Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 1 133 180 km^2 (gross estimate); AOO would be somewhat smaller owing to soil specialisation although moist sandy savanna is widespread across its large EOO; therefore, currently assessed as Least Concern (LC).

Conservation measures: Type material needs to be examined to ensure validity and status of this species in comparison to two close relatives; assessment of conservation status would be improved by quantitative data on vegetation and food associations; protected in uMkhuze and Tembe game reserves (South Africa).

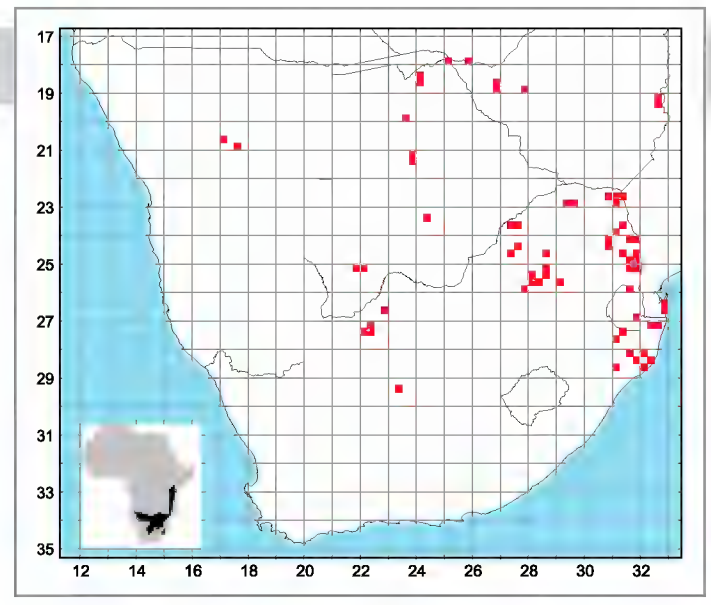
Caccobius nigritulus

(Klug, 1855)

= *Onthophagus litigiosus* Péringuey, 1901

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: As *Onthophagus nigritulus*: 'Sena' [central Mozambique]; *O. litigiosus*: 'Mozambique (Rikatla)' [Ricatla].

Taxonomy: Accepted Group IX species in subgenus, *Caccophilus* Jekel, 1872; *Caccobius upembanus* Frey, 1958, described from 'Kaswabilenga' [SE Democratic Republic of the Congo (DRC)] should be re-examined as a valid taxon or possible further synonym.

Distribution: Widespread in dry to moist sandy savanna from southern to E Africa: South Africa, Mozambique, Zimbabwe, Botswana, Namibia, Angola, Tanzania, Kenya.

Locality data (mean ± SD, range): Altitude: 695 ± 424, 0–1 444 m; annual rainfall: 598 ± 190, 267–1 136 mm; annual temperature (max. + min. /2): 21.1 ± 1.7, 16.8–25.7°C (N=102).

Habitat: In Gauteng bushveld: extreme bias to deep sand (112) compared to sandy clay loam (4) and bias to open woody savanna (79) and shaded thicket (30) compared to grassland (7); similar soil bias in uMkhuze Game Reserve: sand (1.4), sand on clay (0.1), sandy clay loam (0), clay (0); on deep sand in Botswana: extreme bias to moister wooded NE (15 656) than open arid SW (12); largely supported by DBRU collection records: sand (9), sandy loam (4), sandy clay loam (1) in grassland/pasture (4), shrubland (2), open woodland (11), forest (2).

Food types: In Botswana: strong bias to omnivore dung (pig, 10 888) compared to herbivore dung (elephant, 1 783; sheep, 2 200; cattle, 713) or carrion (chicken livers, 72); same bias at Phalaborwa: pig (652), elephant (175), cattle (41); similar bias in Gauteng bushveld: pig (353), horse (2), cattle (40), carrion (1); DBRU collection records reflect common dung types: human/cattle mix (1), elephant (12), rhinoceros (2), zebra (1), horse (1), donkey (1), cattle (9), buffalo (2), wildebeest (1).

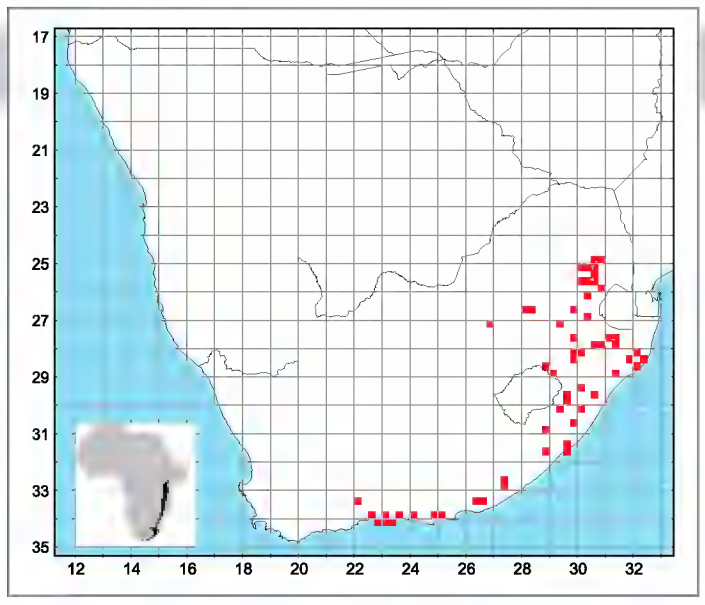
Temporal activity: Diurnal flight activity during the summer rainy season (Oct. to Apr.); in Gauteng bushveld: activity commencing in early summer (Oct.), building to a peak in mid-summer (Dec., Jan.), tailing off to late summer (Apr.); at Phalaborwa: most active during hot, dry weather (653), less so on warm days following heavy rainfall (sunny, 126) or light rainfall (cloudy, 89).

Ecoregions Namibia, Botswana, Zimbabwe, Mozambique: Rare in Kalahari Xeric Savanna (AT1309); more abundant in Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian Baikiaea Woodlands (AT0726), Zambezian and Mopane Woodlands (AT0725), Southern Miombo Woodlands (AT0719); also Maputaland Coastal Forest Mosaic (AT0119).

Bioregions South Africa: Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl), also very low population density in W Eastern Kalahari Bushveld (SVk) (Savanna Biome); also N Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 2 013 940 km² (gross estimate); AOO would be somewhat smaller owing to soil specialisation although sandy soils are widespread across its range; despite a measured bias to omnivore dung, recorded in abundance on other dung types including that of farm livestock; bias to wooded savanna suggests clearance of trees would be detrimental to population density; however, assessed as Least Concern (LC) due to widespread range and protection in various reserves.

Conservation measures: None recommended; protected and abundant in various national parks including: Kruger (South Africa), Chobe (Botswana), Hwange (Zimbabwe).



Caccobius obtusus

(Fahraeus, 1857)

= *Onthophagus mastrucatus* Péringuey, 1901

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Onthophagus obtusus*: 'in terra Natalensi' [KwaZulu-Natal, South Africa]; *O. mastrucatus*: 'Cape Colony (Graham's Town), Natal (Durban)' [South Africa: Eastern Cape, KwaZulu-Natal].

Taxonomy: Accepted Group X species in subgenus, *Caccophilus* Jekel, 1872; sexual dimorphism (head), prominence of characters varies with body size; habitus and aedeagus of *Caccobius cuspidiger* d'Orbigny, 1913 (described from Kenya: 'Afrique orientale anglaise: Kamilito dans le Nandi au nord-est du lac Victoria-Nyanza') are extremely close to *C. obtusus*; review required to investigate possible synonymy.

Distribution: In South Africa: widespread on the moister E parts of the Highveld plus SE and S coasts; also uplands and wet coastal plain of central Mozambique plus uplands of Tanzania, Kenya; n.b. *C. cuspidiger* cited from Kenya, Malawi.

Locality data (mean ± SD, range): Altitude: 1 047 ± 634, 0–2 286 m; annual rainfall: 796 ± 208, 255–1 659 mm; annual temperature (max. + min. /2): 16.6 ± 2.6, 10.6–25.2°C (N=75).

Habitat: No adequate quantitative data; across a 500–2 800 m grassland gradsect in S KwaZulu-Natal: recorded only at 1 000 m (17.0) and 1 500 m (19.9); at Carolina: marginally more abundant in improved Kikuyu pasture (274) and fallow crop field (266) than natural *Themeda* grassland (165); DBRU collection records from sand (2), sandy loam (9), sandy clay loam (10), clay (2), primarily in grassland/pasture (20), also open woodland (2), fallow crop field (1).

Food types: No quantitative assessment; DBRU collection records primarily from dung of cattle (23), also elephant (1), horse (1).

Temporal activity: Diurnal flight activity, primarily during the summer rainy season (Oct. to May).

Bioregions South Africa: Centred on N and E Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs) (Grassland Biome) plus Indian Ocean Coastal Belt Biome (CB); also S coastal localities in Fynbos Biome (probably disturbed and replaced by pasture).

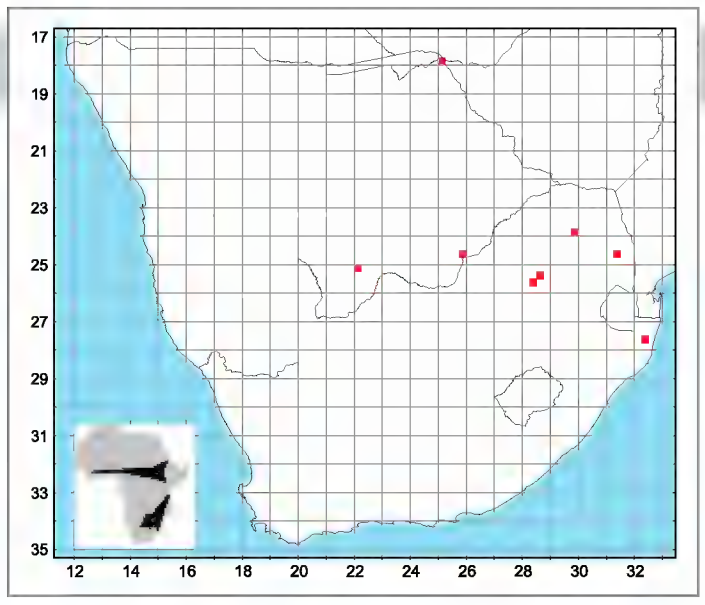
Assessment rationale: EOO = 781 120 km^2 (gross estimate); AOO smaller, centred on moist cool uplands and moist coastal regions; recorded at forest localities, but presumably primarily in grassland although quantitative support is lacking; readily attracted to dung of domestic livestock and tolerant of habitat modification in farmland; assessed as Least Concern (LC)

Conservation measures: Assessment of conservation status would be improved by review of taxonomic status and EOO plus quantitative data on ecological associations; protected in Ithala Game Reserve, Mt Sheba Nature Reserve (South Africa).

Genus *Cleptocaccobius* Cambefort, 1984

Type species and designation: *Caccobius* (*Caccophilus*) *signaticollis* d'Orbigny, 1902, by original designation.
Synonyms: None.
Last review: Entire genus created and reviewed by Cambefort (1984); new species added by Cambefort (1985b), Josso and Prévost (2006b).

Cleptocaccobius Cambefort, 1984, was created by raising Group XI of *Caccobius* Thomson, 1859 to generic level (Cambefort 1979). It currently comprises 23 small-bodied species found in the Afrotropical (15) and Oriental regions (7) with one shared between the Afrotopical and Palaearctic regions (Arabian Peninsula). Species accounts are provided for three species recorded from South Africa, Botswana and Namibia although three other species were recognised in collections from southern Africa that could not be named with confidence.



Cleptocaccobius convexifrons

(Raffray, 1877)

= *Onthophagus pudens* Péringuey, 1901
= *Caccobius viridicollis* Fahraeus, 1857, *sensu* d'Orbigny, 1902
= *Caccobius viridicollis* Fahraeus var. *picipennis* d'Orbigny, 1902

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Onthophagus convexifrons*: 'Ile de Zanzibar' [Zanzibar, Tanzania]; *O. pudens*: 'Southern Rhodesia (Salisbury)' [Harare, Zimbabwe]; *C. viridicollis sensu* d'Orbigny: Not stated; var. *picipennis*: 'l'Afrique orientale allemande: Bagamoyo' [Bagamoyo, Tanzania].

Taxonomy: Accepted kleptocoprid species.

Distribution: Widespread in moist sandy savanna from S to E and E to W Africa: South Africa, Botswana, Zimbabwe, Tanzania, Kenya; also cited from Democratic Republic of the Congo (DRC), Eritrea, Côte d'Ivoire, Mauritania.

Locality data (mean ± SD, range): Altitude: 806 ± 360, 55–1 272 m; annual rainfall: 622 ± 124, 283–751 mm; annual temperature (max. + min. /2): 21.0 ± 2.0, 16.8–24.4°C (N=12).

Habitat: In Gauteng bushveld: extreme specialisation to deep sand (524) compared to sandy clay loam (6) with a bias to more open vegetation: grassland (201), open woodland (241), shaded thicket (88); in Botswana: common in moist NE (3 203), rare in arid SW (1).

Food types: In Botswana: abundant on various dung types although showing clear bias: sheep (1 927), pig (820), cattle (281), elephant (142), also chicken liver carrion (33).

Temporal activity: Flight activity in darkness during the summer rainy season (Oct. to Apr.); in Gauteng bushveld: primarily active early in the rainy season (Oct., Nov.) with activity continuing at lower levels until end of Mar.

Ecoregions Botswana: Zambezian and Mopane Woodlands (AT0725), Kalahari Acacia-Baikiaea Woodlands (AT0709), Kalahari Xeric Savanna (AT1309).

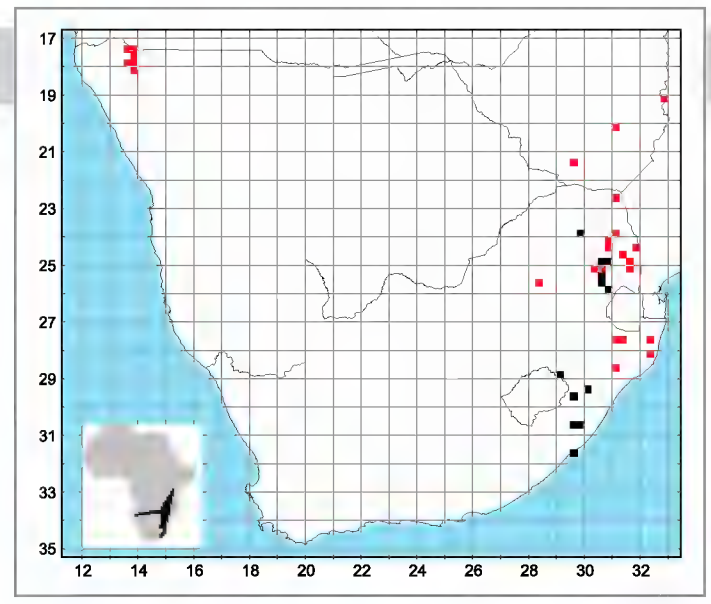
Bioregions South Africa: Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 3 973 335 km^2; AOO would be much smaller owing to soil specialisation on deep sands; however, widespread and locally abundant; low number of localities would be a collection artefact due to small body size; assessed as Least Concern (LC).

Conservation measures: No conservation measures necessary at present; protected in Leeuwfontein Nature Reserve (South Africa), Chobe National Park (Botswana).

Cleptocaccobius postlutatus

(d'Orbigny, 1905)



No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Caccobius postlutatus*: 'Afrique orientale anglaise: Nairobi' [Nairobi, Kenya].

Taxonomy: Accepted kleptocoprid species, but material cited here as *C. postlutatus* requires validation; highland and lowland populations of southern Africa indistinguishable; minor sexual dimorphism (head).

Distribution: Putative widespread range in moist lowland woodland and highland grassland or forest, from S to E Africa: South Africa, Zimbabwe, Mozambique, Kenya; lowland range (red squares); highland range (black squares).

Locality data (mean ± SD, range): Altitude: 885 ± 567, 0–2 274 m; annual rainfall: 724 ± 212, 356–1 157 mm; annual temperature (max. + min. /2): 18.9 ± 3.4, 10.6–25.2°C (N=51).

Habitat: No quantitative assessment; DBRU collection records from finer-grained soils (sandy loam: 3; sandy clay loam: 3; clay: 1) in highland pasture (2), lowland woodland (5), plantation (1).

Food types: No quantitative assessment; DBRU collection records from dung of cattle (4), elephant (4), donkey (1), human (1).

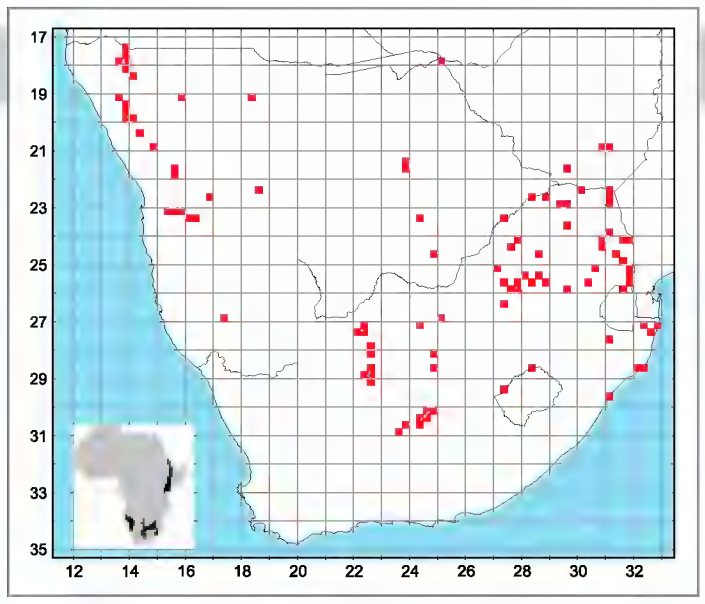
Temporal activity: Diel flight periodicity unknown; active in the summer rainy season (Oct. to Apr.).

Ecoregions Namibia, Zimbabwe: N Namibian Savanna Woodlands (AT1316), Zambezian and Mopane Woodlands (AT0725), Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Centred on Lowveld (SVl) (Savanna Biome); N and E edge Mesic Highveld Grassland (Gm), N Sub-Escarpment Grassland (Gs) (Grassland Biome); Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 1 627 085 km^2 (gross estimate); AOO would be smaller assuming indications of soil (finer-grained) and vegetation associations (lowland woodland, highland grassland) are supported by quantitative data; however, putative widespread occurrence justifies an assessment of Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by validation of species identity, further distribution data and quantitative data on ecological associations; lowland population protected in Kruger National Park (South Africa), highland populations in the Cathedral Peak area of N uKhahlamba Drakensberg Park (World Heritage Site) (South Africa).



Cleptocaccobius viridicollis

(Fahraeus, 1857)

= *Caccobius minimus* d'Orbigny, 1898
= *Caccobius viridicollis* Fahraeus, 1857, var. *semicoeruleus* d'Orbigny,1905

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Onthophagus viridicollis*: 'prope fluvium Gariep' [near Orange River, South Africa]; *C. minimus*: 'Arabie: Yemen' [Yemen]; var. *semicoeruleus*: 'Afrique orientale anglaise: Tavéta, Boura, Mwataté, Voi....Sambouru' [E Kenya].

Taxonomy: Accepted kleptocoprid species; synonym from Yemen assumed valid.

Distribution: Mostly arid to dry savanna from S to NE Africa with a synonym described from S Arabia (Yemen): South Africa, Botswana, Namibia, Zimbabwe, E Kenya; also cited from Mozambique, Malawi, Tanzania, Somalia, Ethiopia, Eritrea; disjunctions may be partly a collection artefact related to very small body size and partly due to unsuitable conditions.

Locality data (mean ± SD, range): Altitude: 971 ± 417, 0–1 830 m; annual rainfall: 448 ± 208, 88–1 004 mm; annual temperature (max. + min. /2): 19.1 ± 2.5, 13.3–24.4°C (N=134).

Habitat: In Gauteng bushveld: bias to finer-grained soils in open woody vegetation, deep sand (603), sandy clay loam (1 628), grassland (645), open woodland (1 403), shaded thickets (173); in uMkhuze Game Reserve: strong bias to coarse-grained soils, deep sand (21.4), sand on clay (4.8), sandy clay loam (0.3), clay (0.6); partly supported by DBRU collection records from sand (5), sandy loam (8), sandy clay loam (4) in grassland/pasture (3), scrub/shrubland (7), open woodland (7).

Food types: At Phalaborwa: bias to dung of omnivores (pig: 758), and ruminant herbivores (cattle: 328), least to monogastric herbivores (elephant: 81); in Gauteng bushveld: somewhat similar trend (pig: 21, cattle: 9, horse: 11); DBRU collection records from dung of cattle (12), donkey (2).

Temporal activity: Diurnal flight activity in the summer rainy season (Oct. to Apr.); in Gauteng bushveld: diel peak in flight in the late morning (10:00–12:00), declining after midday (12:00–14:00) and seasonal peak early rainy season (Oct., Nov.) becoming lower in mid-summer (Dec., Feb.) and very low in late summer (Mar., Apr.); at Phalaborwa: most abundant on a hot, dry day (559), remaining relatively abundant on a warm, cloudy day following light rainfall (288) or a warm, sunny day soon after heavy rainfall (263).

Ecoregions Namibia, Botswana, Zimbabwe: Namibian Savanna Woodlands (AT1316), Kalahari Xeric Savanna (AT1309), Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian and Mopane Woodlands (AT0725), marginal occurrence in three other ecoregions.

Bioregions South Africa: Primarily Eastern Kalahari Bushveld (SVk), Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome); also E Upper Karoo (NKu) (Nama Karoo Biome); marginal occurrence in three other bioregions.

Assessment rationale: EOO = 1 295 810 km^2 (African mainland range only; assumed disjunct); widespread with fairly generalist ecological associations; much of range coincides with little-transformed areas; assessed as Least Concern (LC).

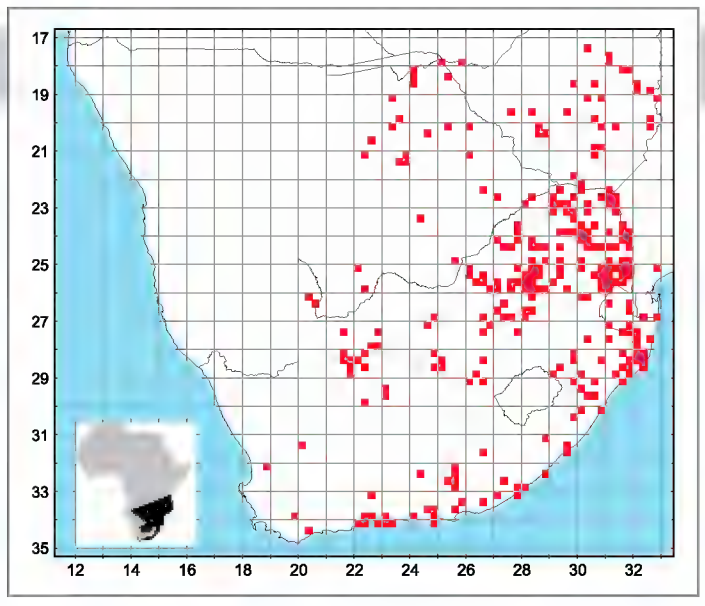
Conservation measures: Assessment of conservation would be improved by further quantitative data on soil and dung type associations to resolve slight conflicts in existing data; protected in Kruger National Park (South Africa).

Genus *Digitonthophagus* Balthasar, 1959

Type species and designation: *Scarabaeus bonasus* Fabricius, 1775, by original designation.
Synonyms: None.
Last review: Entire genus reviewed by Génier and Moretto (2017).

Until recently, *Digitonthophagus* Balthasar, 1959, has been considered to comprise only two species. However, a recent revision has determined that one of the taxa comprises a species complex. Therefore, the number of species has now been raised to 16 found in the Afrotropical (12) and Oriental regions (2) or shared between the W Oriental and S Palaearctic (Afghanistan) (1), or, Afrotropical and S Palaearctic (Arabian Peninsula) (1). One of the Afrotropical species is also widely represented in Madagascar probably due to introduction from E Africa.

Three species are represented in southern Africa. One is widespread in dry to moist savannas of South Africa, Botswana and Namibia ranging into the E tropics. Two are restricted to the W, one to the N in dry NW Namibia, W Angola, and W Democratic Republic of the Congo (DRC), one to the S in arid W South Africa and W Namibia, overlapping with the other species in NW Namibia and SW Angola. All three are common tunnelling species that are assessed as Least Concern (LC).



Digitonthophagus gazella

(Fabricius, 1787) auctorum

= *Scarabaeus dorcas* Olivier, 1789

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Scararabaeus gazella*: Not stated; *S. dorcas*: 'Madagascar'.

Taxonomy: Accepted species, but recent revision (Génier & Moretto 2017) shows that in its original sense *S. gazella* [=*D. gazella*] is a junior synonym of *Scarabaeus catta* Fabricius, 1787, described from 'Coromandel' [E India]; as the species described as *S. dorcas* [=*Digitonthophagus dorcas*] has been widely introduced into the Americas, Australia and Japan under the species name *gazella*, a case has been made to suppress the original affiliation of *S. gazella*, conserve the modern name, *Digitonthophagus gazella*, for the introduced species (ICZN case no. 3722) and make *S. dorcas* [=*D. dorcas*] a junior synonym; sexually dimorphic (head, disc of prothorax); prominence of characters varies with body size.

Distribution: Widespread in grasslands and grassland savannas of S Central and SE Africa: South Africa, Botswana, NE Namibia, Zimbabwe, Mozambique, SW Angola, Zambia, S Democratic Republic of the Congo (DRC), Tanzania, SE Kenya; also widespread in Madagacar where it was probably introduced by accident about 1 000 yrs ago (Rahagala et al. 2009); widely introduced intentionally into Australia, S USA (range expanded S through central America), South America and Japan; also recently into New Zealand.

Locality data (mean ± SD, range): Altitude: 804 ± 478, 0–1 760 m; annual rainfall: 626 ± 211, 149–1 659 mm; annual temperature (max. + min. /2): 19.5 ± 2.3, 13.5–25.2°C (N=404).

Habitat: In Gauteng bushveld: bias to finer-grained soils (sandy clay loam, 310; deep sand, 92) and open vegetation (grassland: 302; open woodland: 73; shaded thicket: 27); limited soil bias in uMkhuze Game Reserve: deep sand (1.6), sand on clay (3.1), sandy clay loam (3.0), clay (1.8); DBRU collection records on sand (25), sandy loam (19), sandy clay loam (34), clay (16) in grassland/pasture (47), scrub/shrubland (13), open woodland (14), shaded thicket (2), also fallow crop fields (3).

Food types: On deep sand in Botswana: bias to herbivore dung (elephant, 25; cattle, 21; sheep, 48) compared to omnivore dung (pig, 7) and carrion (chicken livers, 0); but on sandy loam at Phalaborwa: slight bias to omnivore dung (pig, 182) compared to herbivore dung: monogastric (elephant, 144), ruminant (cattle, 76); DBRU collection records on dung of cattle (101), buffalo (2), elephant (5), zebra (4), horse (4), donkey (1), human (1), human/buffalo mix (1).

Temporal activity: Flight activity in darkness during the summer rainy season (Oct. to Apr.); also Aug., May, mostly at warmer coastline; in Gauteng bushveld: active early to late summer (Oct. to Feb.) tailing off in Mar., rare in Apr.; at Phalaborwa: most active on a warm evening soon after heavy rainfall (232), less so on warm evenings after cloudy weather with light rain (89) or hot, dry weather (80); attracted to light.

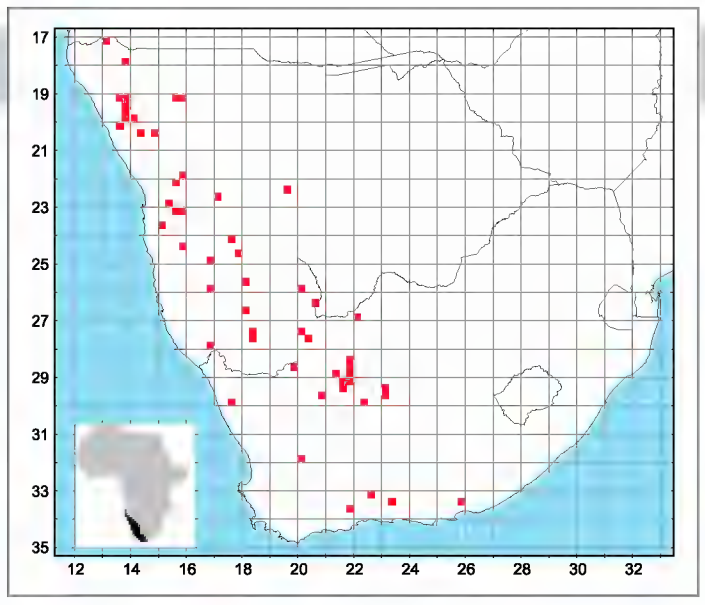
Ecoregions Botswana, Zimbabwe, Mozambique: SE Kalahari Xeric Savanna (AT1309), Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian and Mopane Woodlands (AT0725), Southern African Bushveld (AT0717), Southern Miombo Woodlands (AT0719),

Maputaland Coastal Forest Mosaic (AT0119), marginal records in one other ecoregion.

Bioregions South Africa: Centred on Kalahari Duneveld (SVkd), Eastern Kalahari Bushveld (SVk), Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome); Dry Highveld Grassland (Gh), Sub-Escarpment Grassland (Gs) (Grassland Biome); Indian Ocean Coastal Belt Biome (CB), Albany Thicket Biome (AT); occurrence in Fynbos Biome possibly due to range expansion in response to clearance of natural vegetation.

Assessment rationale: EOO = 3 711 400 km^2 (African mainland only); widespread in open vegetation; apparent slight bias to finer-grained soils and possibly herbivore dung; widely introduced into other continents; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by further quantitative data to resolve slight conflicts in soil and dung type association; protected in many national parks, including Kruger (South Africa), Gorongosa (Mozambique).



Digitonthophagus namaquensis

Génier, 2017

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Farm Klipkoppies (6) (28.87137 S 21.30944 E), 957 m, Northern Cape, South Africa'.

Taxonomy: Accepted species; sexually dimorphic (head, disc of prothorax); prominence of characters varies with body size.

Distribution: Arid late summer rainfall region of SW Africa: South Africa, Namibia, SW Angola.

Locality data (mean ± SD, range): Altitude: 984 ± 261, 249–1 730 m; annual rainfall: 215 ± 89, 22–424 mm; annual temperature (max. + min. /2): 18.3 ± 2.1, 14.9–22.2°C (N=69).

Habitat: No quantitative assessment; DBRU collection records from sand (6), sandy loam (2), sandy clay loam (3) in scrub (9), open woodland (2).

Food types: No quantitative assessment; DBRU collection records from dung of cattle (5), buffalo (1), wildebeest (1), zebra (2), horse (1), donkey (1).

Temporal activity: Flight activity in darkness during the late summer rainy season (Dec. to May), attracted to light.

Ecoregions Namibia: Succulent Karoo (AT1322), Namib Desert (AT1315), Namibian Savanna Woodlands (AT1316), SW Kalahari Xeric Savanna (AT1309), Angolan Mopane Woodlands (AT0702).

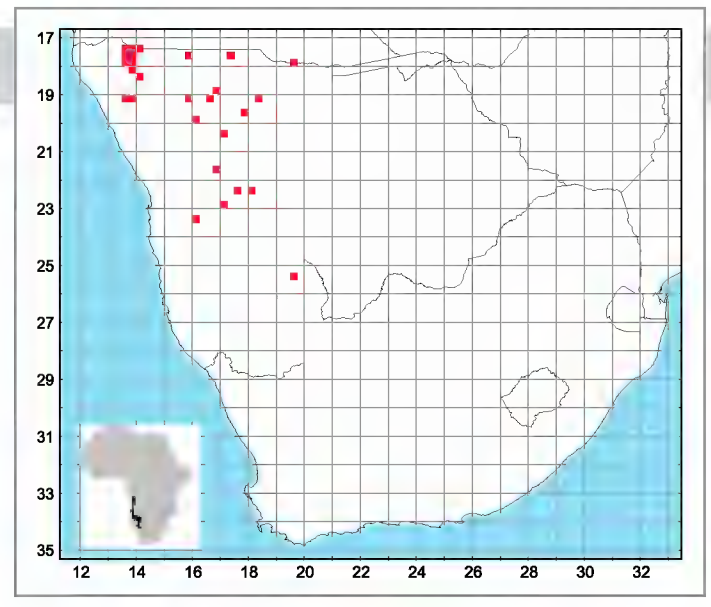
Bioregions South Africa: Kalahari Duneveld (SVkd) (Savanna Biome); Bushmanland (NKb) (Nama Karoo Biome); Namaqualand Hardeveld (SKn), Trans-Escarpment Succulent Karoo (SKt), Rainshadow Valley Karoo (SKv) (Succulent Karoo Biome); Albany Thicket Biome (AT).

Assessment rationale: EOO = 795 870 km^2; widespread in little-transformed arid regions of SW Africa used primarily for grazing of domestic livestock or conservation of indigenous fauna; not, therefore, facing any threats; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative ecological data; protected in Kgalagadi Transfrontier Park (South Africa), Etosha National Park (Namibia).

Digitonthophagus viridicollis

Génier, 2017



No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Moanda, Zaïre' [Moanda, W Democratic Republic of the Congo (DRC)].

Taxonomy: Accepted species although Génier and Moretto (2017) note that separation from *D. gazella* (Fabricius, 1787) *auctorum* at species level may not be justified as differences are geographically consistent, but limited; sexually dimorphic (head, disc of prothorax); prominence of characters varies with body size.

Distribution: Dry savanna, W extremes of South central Africa: N Namibia, W Angola, W margins of Democratic Republic of the Congo (DRC).

Locality data (mean ± SD, range): Altitude: 1 222 ± 300, 683–1 998 m; annual rainfall: 390 ± 117, 125–623 mm; annual temperature (max. + min. /2): 19.6 ± 2.2, 16.3–23.0°C (N=29).

Habitat: No quantitative assessment; DBRU collection records from sand (2), sandy loam (2), sandy clay loam (3) in grassland (2), shrubland (2), open woodland (3).

Food types: No quantitative assessment; DBRU collection records from dung of cattle (7).

Temporal activity: Flight activity in darkness during the summer rainy season (Nov. to Apr.), attracted to light.

Ecoregions Namibia: Namibian Savanna Woodlands (AT1316), Angolan Mopane Woodlands (AT0702), W Kalahari Xeric Savanna (AT1309), W Kalahari Acacia-Baikiaea Woodlands (AT0709), W Zambezian Baikiaea Woodlands (AT0726).

Assessment rationale: EOO = 419 910 km^2; widespread; possibly, generalist soil and vegetation associations; recorded on dung of domestic livestock; probably not threatened by clearance of woodland, but quantitative data required in support; currently assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative ecological data; protected in Etosha National Park (Namibia).

Genus *Euonthophagus* Balthasar, 1959

Type species and designation: *Scarabaaeus amyntas* Olivier, 1789, by original designation.
Synonyms: None.
Last review: Genus created and reviewed by Balthasar (1959); valid new Afrotropical species added by Cambefort (1972).

Euonthophagus Balthasar, 1959, was created by raising Group 8 (d'Orbigny 1913) of *Onthophagus* Latreille, 1802, to generic level. It currently comprises 36 valid species in the Palaearctic (20) and Afrotropical regions (16). As the differences between species are often subtle, some Afrotropical species undoubtedly remain undescribed whereas others have been wrongly synonymised. A revision of the Afrotropical species is necessary.

Nine *Euonthophagus* species were recognised in collections from South Africa, Botswana and Namibia. Five of these species remain unnamed and it is unclear which, if any, remain undescribed. It was not possible to match them to existing species names although two have been described from South Africa in addition to those recognised below in species accounts, one valid, one a synonym.

Species accounts are presented for only four species of which only two were described from South Africa. Of the four species, three are valid whereas one is considered valid, but officially remains a synonym. These four species are centred on the Upper Karoo, SW Kalahari, southern savanna, E savanna ranging into the E tropics. All are locally abundant and none is considered threatened although one has been recorded only on monograstic herbivore dung in game reserves.

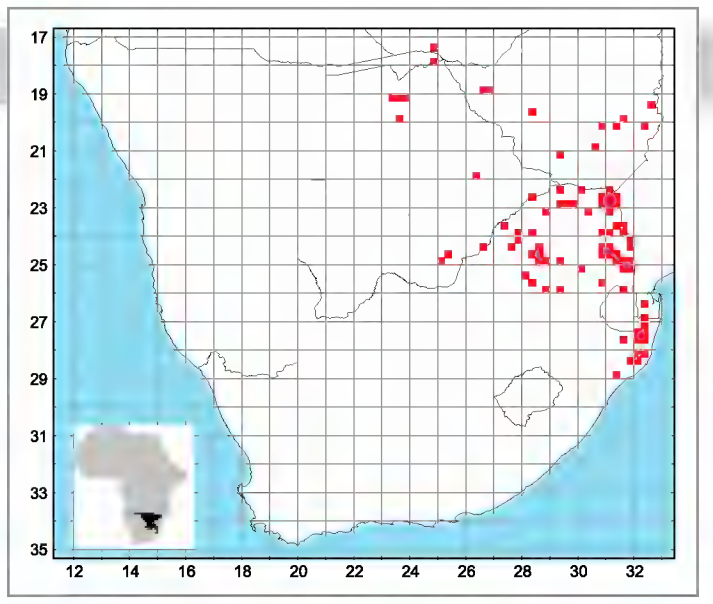
Euonthophagus carbonarius

(Klug, 1855)

= *Onthophagus aterrimus* Gerstaecker, 1871
= *Onthophagus interstitialis* Fahraeus, 1857, *sensu* Gestro, 1895
= *Onthophagus glaber* Boheman, 1857 (nec Fahraeus), *sensu* Péringuey, 1901
= *Onthophagus vicarius* Péringuey, 1901 (synonymised in error)

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: As *Onthophagus carbonarius*: 'Sena' [central Mozambique]; *O. aterrimus*: 'See Jipe und dem Bura-Bergen' [Kenya: Lake Jipe and Bura Mts]; *O. interstitialis sensu* Gestro: 'Ganale Guddá' [Ethiopia]; *O. glaber sensu* Péringuey: 'Transvaal (Rustenburg)' [North-West Province, South Africa]; *O. vicarius*: 'Cape Colony (Beaufort West)' [Beaufort West, Western Cape, South Africa].

Taxonomy: Accepted species, but extensive history of confusion with very close relatives; minor sexual dimorphism, varying with body size (head, prothoracic disc); synonyms require validation as all have likely been synonymised in error; *O. vicarius* synonymy certainly an error (see species account: *Euonthophagus vicarius* (Péringuey, 1901)); citation of 'Cape Colony (Griqualand West)' [central Northern Cape, South Africa] as a second locality for *O. glaber sensu* Péringuey may represent confusion with *E. vicarius*.

Distribution: Centred on moist, sandy, lowland savanna, S Central and SE Africa: NE South Africa, E Botswana, S Angola, S Zambia, S and N Zimbabwe, central and S Mozambique; following records are *all* errors: Arabian Peninsula, Mauritania, Senegal, Sudan, Ethiopia, Eritrea, Kenya, Tanzania and Cape Province of South Africa.

Locality data (mean ± SD, range): Altitude: 627 ± 417, 11–1 899 m; annual rainfall: 619 ± 146, 304–1 121 mm; annual temperature (max. + min. /2): 21.3 ± 1.9, 13.1–25.7°C (N=115).

Habitat: No adequate quantitative assessment; DBRU collection records suggest a bias to sandy soils: sand (35), sandy loam (21), sandy clay loam (11), clay (1) in woodland: grassland/pasture (6), shrubland (9), open woodland (42), forest/thickets (6).

Food types: At Phalaborwa: primarily attracted to omnivore (pig: 3 930) or monogastric herbivore dung (elephant: 2 697), less to ruminant herbivore dung (cattle: 625); DBRU collection records from various dung types: human or human cattle mix (6), elephant (18), rhinoceros (5), horse (2), donkey (1), zebra (3), warthog (1), cattle (33), buffalo (3), wildebeest (1), waterbuck (1).

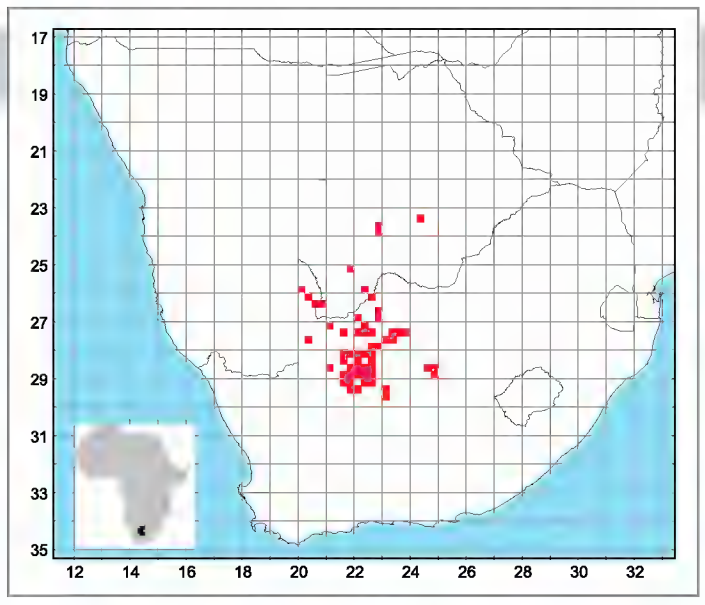
Temporal activity: Flight activity in darkness primarily during the summer rainy season, but recorded in all months except Sept. reflecting its lowland centre of distribution; attracted to light; at Phalaborwa: primarily active on evenings after a hot, dry day (3 954), less on an evening following a warm cloudy day with light rainfall (2 319) or an evening following a warm day a few days after heavy rainfall (1 028).

Ecoregions Botswana, Zimbabwe, Mozambique: E Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian & Mopane Woodlands (AT0725), Southern African Bushveld (AT0717), S Southern Miombo Woodlands (AT0719), Maputaland Coastal Forest Mosaic (AT0119).

Bioregions South Africa: Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 946 605 km^2 (gross estimate); widespread EOO, but AOO may be restricted by soil, vegetation and dung type specialisation so that clearance of woodland on sand in farmland may be detrimental to population density; however, locally abundant, particularly in game reserves where 64% (68 out of 106) of DBRU records were made; observed flying in large numbers to elephant dung at dusk in Bicuar National Park (Angola); assessed as Least Concern (LC) owing to wide range and widespread protection.

Conservation measures: Assessment of conservation status would be improved by quantitative data on habitat associations; protected in various national parks and game reserves: Kruger, uMkhuze, Hluhluwe–iMfolozi (South Africa); Hwange (Zimbabwe), Bicuar (Angola), Moremi (Botswana).



Euonthophagus flavimargo

(d'Orbigny, 1902)

No synonyms

Global: LC
Endemic: RSA, Botswana

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: as *Onthophagus flavimargo*: 'Natal' [KwaZulu-Natal, South Africa].

Taxonomy: Accepted species, but cited type locality probably an error as it lies far outside of the known range of the species.

Distribution: Deep sands of dry to arid SW Kalahari: Botswana, South Africa.

Locality data (mean ± SD, range): Altitude: 1 080 ± 130, 764–1 467 m; annual rainfall: 264 ± 60, 142–419 mm; annual temperature (max. + min. /2): 19.3 ± 0.7, 17.6–21.2°C (N=114).

Habitat: No adequate quantitative data; in Northern Cape: high frequency in SW Kalahari, mainly on deep sands (86.7%, 85 out of 98 samples), low frequency in uplands to S of Orange River (5.8%, 7/121) and in NE Bushmanland (13.4%, 9/67); DBRU collection records almost exclusively on sand (12), also sandy clay loam (1) in grassland (5), scrub/shrubland (6), open woodland (2).

Food types: In Botswana: bias to dung of omnivores (pig: 71) and monogastric herbivores (elephant: 55) compared to ruminant herbivores (cattle: 11; sheep: 26), not in carrion (chicken livers: 0); DBRU collection records on dung of cattle (11), donkey (1).

Temporal activity: Flight activity in darkness, primarily during the late summer rainy season (Dec. to May, also Oct.).

Ecoregions Botswana: SE Kalahari Xeric Savanna (AT1309).

Bioregions South Africa: Kalahari Duneveld (SVkd), W and S Eastern Kalahari Bushveld (SVk) (Savanna Biome); extreme NE Bushmanland (NKb) (Nama Karoo Biome).

Assessment rationale: EOO = 211 965 km^2; although quantitative support is required, AOO probably limited by occurrence of deep sand, which nevertheless covers most of the large EOO; range restricted to a little-transformed region used primarily for conservation and grazing of farm livestock to which it is attracted despite a measured bias to omnivore and indigenous herbivore dung; assessed as Least Concern ((LC).

Conservation measures: Assessment of conservation status would be improved by further quantitative data on habitat associations; protected in Kgalagadi Transfrontier Park (South Africa/Botswana).

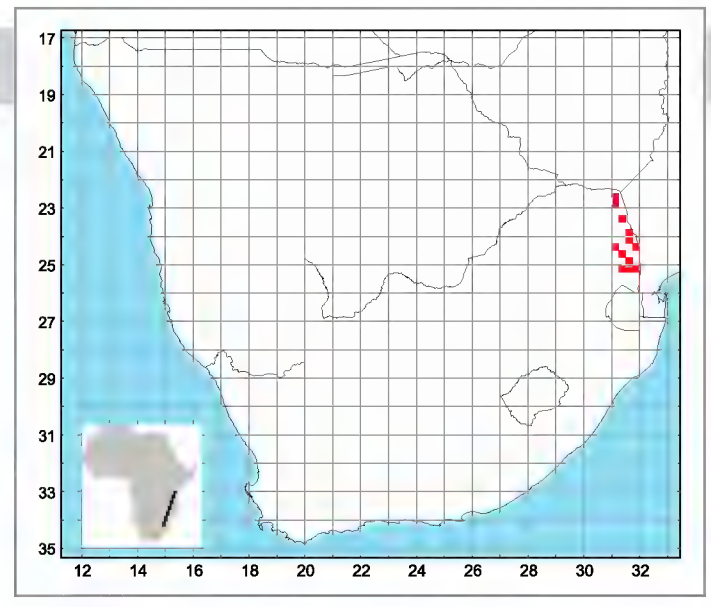
Euonthophagus jeanneli

(d'Orbigny, 1913)

= *Onthophagus tibialis* Frey, 1963
= *Onthophagus tibialis diversiceps* Frey, 1975b

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: As *Onthophagus jeanneli*: 'Afrique orientale anglaise: Tavéta.....; Afrique orientale allemande: rivière Himo sur le versant sud-est du Kilimandjaro' [Taveta, Kenya; Himo River, Tanzania]; *O. tibialis*: 'Makindu, Kongo' [possibly an error for Makindu, Kenya]; *O. tibialis diverciceps*: 'Krueger Nationalpark: Skukuza, Satara, Pundamilia' [Kruger National Park, South Africa].

Taxonomy: Accepted species; *O. tibialis diversiceps* not formally synonymised; status and origin of *O. tibialis* Frey, 1963 needs further examination; minor sexual dimorphism.

Distribution: Patchy occurrence owing to monogastric dung association in hot, dry savanna on the E seaboard of Africa: South Africa, Kenya, Tanzania.

Locality data (mean ± SD, range): Altitude: 371 ± 102, 153–576 m; annual rainfall: 582 ± 100, 458–788 mm; annual temperature (max. + min. /2): 22.4 ± 0.9, 20.7–23.5°C (N=19).

Habitat: No quantitative assessment; at South African Wildlife College: recorded in very open savanna on coarser granite (2.6) and finer gabbro-derived soils (3.8) within the Kruger National Park; much less abundant in adjoining communal farm rangeland (0.8, 0.3); severely limited DBRU collection records from sandy loam (3) in shrubland (1), open woodland (1).

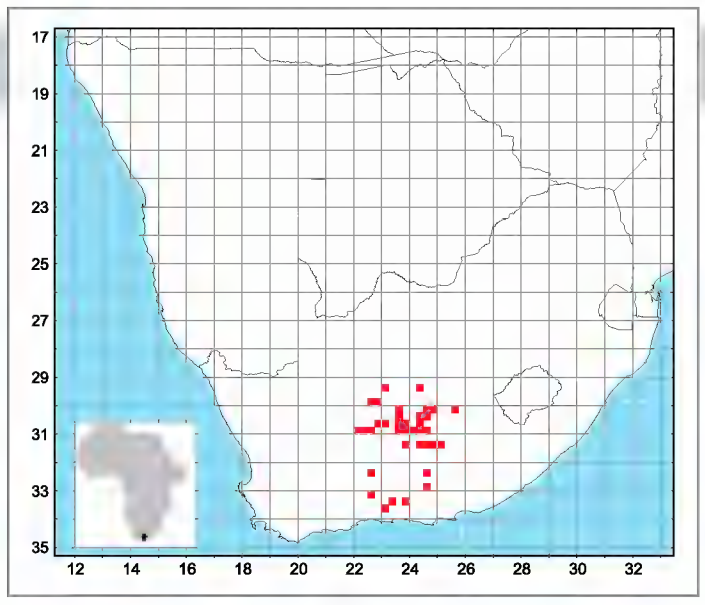
Food types: No quantitative assessment; all DBRU collection records from coarse-fibred, monogastric herbivore dung; elephant (13), zebra (1).

Temporal activity: Diel flight periodicity unknown, active during the summer rainy season (Nov. to Mar.).

Bioregions South Africa: Mopane (SVmp), Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 409 200 km^2 (gross estimate, possibly larger); AOO would be much smaller and dependent on occurrence of large monogastric herbivores from whose dung all known records have been made; possibility of soil or vegetation specialisation not tested; despite small known AOO, nearly all modern records are from two large national parks; therefore, currently assessed as Least Concern (LC), although this would change if elephant populations came under increasing threat.

Conservation measures: Assessment of conservation status would be much improved by a survey of elephant dung in savanna along the E seaboard of Africa to determine if the disjunct pattern is real or a collecting artefact; further quantitative data is required on ecological associations, and further work on the effects of range contraction of large monogastric herbivores; protected in Kruger National Park (South Africa), Tsavo East National Park (Kenya).



Euonthophagus vicarius

(Péringuey, 1901)

No synonyms (but see Taxonomy)

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: as *Onthophagus vicarius*: 'Cape Colony (Beaufort West)' [Beaufort West, Western Cape, South Africa].

Taxonomy: Requires formal revalidation; currently synonymised in error with *Euonthophagus carbonarius* (Klug, 1855) described from 'Sena' [central Mozambique].

Distribution: Centred on upland Karoo in the S of the arid, late summer rainfall region (climates III1, II(III)a, II4a – Walter & Lieth 1964) and dry parts of spring/autumn, bimodal rainfall region (climate III5): South Africa.

Locality data (mean ± SD, range): Altitude: 1 236 ± 233, 564–1 598 m; annual rainfall: 282 ± 51, 197–439 mm; annual temperature (max. + min. /2): 15.8 ± 1.2, 14.0–18.9°C (N=64).

Habitat: No adequate quantitative assessment; in Northern Cape: recorded with high frequency in Upper Karoo (70.6%, 48 out of 68 samples), frequency much lower in uplands to S of Orange River (19.0%, 23/121), but abundance similar in samples with *E. vicarius* (3.1 or 3.6/sample), rare in SW Kalahari, absent from low altitude in Bushmanland; abundance/sample similar on sand (2.4), sandy loam (3.6), sandy clay loam (3.4); DBRU collection records on sand (3), sandy loam (5), sandy clay loam (6), clay (1) in grassland/pasture (2), scrub/shrubland (10), open woodland (2).

Food types: No quantitative assessment; DBRU collection records on dung of cattle (12), horse (2).

Temporal activity: Diel flight periodicity unknown, but presumably flies in darkness like other *Euonthophagus* spp.; recorded during spring (Sept.) and late summer rainy seasons (Dec. to Mar.).

Bioregions South Africa: Upper Karoo (NKu) (Nama Karoo Biome), Rainshadow Valley Karoo (SKv) (Succulent Karoo Biome), margins of four adjoining bioregions.

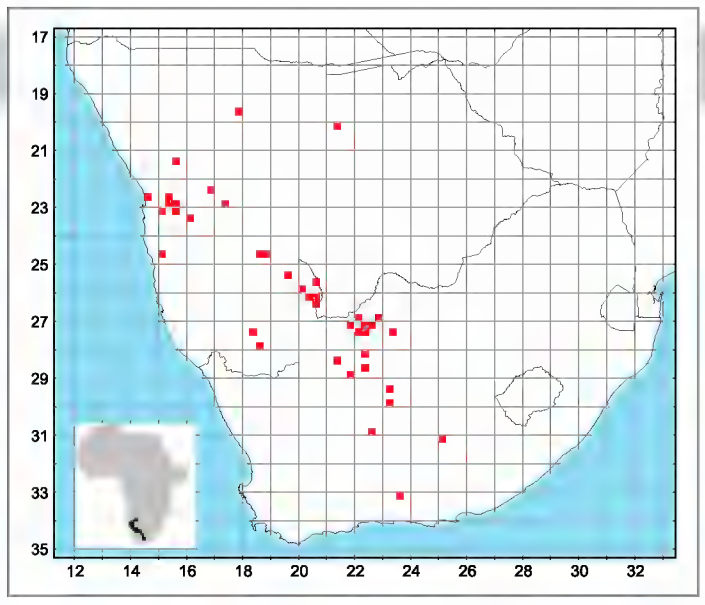
Assessment rationale: EOO = 97 405 km^2; widespread across a little-transformed range used primarily for grazing of farm livestock; recorded with high frequency during a survey of the Upper Karoo; assessed as Least Concern (LC) despite absence of known protection.

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; currently not known from any protected area; a survey of upland areas in Karoo National Park would be worthwhile.

Genus *Hamonthophagus* Roggero, Dierkens, Barbero & Palestrini, 2016

Type species and designation: *Onthophagus bituberculatus* Olivier, 1789, by original designation.
Synonyms: None.
Last review: Genus created and reviewed by Roggero et al. (2016).

Hamonthophagus Roggero, Dierkens, Barbero & Palestrini, 2016, comprises five species recently excised from Group 32 of Afrotropical *Onthophagus* Latreille, 1803, as defined by d'Orbigny (1913). These species are distributed throughout arid to dry savannas from S to E to W Africa. Three species are represented in southern Africa: one in the arid SW; two in savanna with representation also in the E tropics.



Hamonthophagus acutus

(d'Orbigny, 1908)

= *Onthophagus bituberculatus* Boheman, 1860

Global: LC
Endemic: RSA, Botswana, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Onthophagus acutus*: 'lac Ngami..... Okahandya.... Salem' [Botswana: Lake Ngami; Namibia: Okahandja and Salem]; *O. bituberculatus* [pre-occupied name] 'in vicinitate fluviorum Svakop et Kuisip' [Namibia: vicinity of Swakop and Kuiseb rivers].

Taxonomy: Accepted species recently transferred from *Onthophagus* Group 32 of d'Orbigny (1913); some type localities would, presumably, relate to a close relative (*H. fallax* d'Orbigny, 1913): i.e. 'région de Mpala.....Nyassa' [Mpala region, Tanzania; Lake Malawi region]; this type material was not examined in the recent review of Roggero et al. (2016) as it could not be located.

Distribution: Widespread in the S and central arid late summer rainfall region: central SW South Africa, W Botswana, Namibia; records from Malawi, Tanzania, Democratic Republic of the Congo (DRC) remain unvalidated and likely represent confusion with *H. fallax*.

Locality data (mean ± SD, range): Altitude: 1 005 ± 315, 58–1 840 m; annual rainfall: 219 ± 109, 14–532 mm; annual temperature (max. + min. /2): 19.1 ± 1.9, 13.4–22.9°C (N=50).

Habitat: No quantitative assessment; limited DBRU collection records on sand (6), sandy loam (1), sandy clay loam (1) in scrub/shrubland (6); also in pasture (1), open woodland (1).

Food types: No quantitative assessment; limited DBRU collection records on dung of cattle (7), wildebeest (1).

Temporal activity: Flight activity in darkness primarily during the summer rainy season (Sept. to May).

Ecoregions Namibia, Botswana: Succulent Karoo (AT1322), central Namib Desert (AT1315), S Namibian Savanna Woodlands (AT1316), SW Kalahari Xeric Savanna (AT1309), margins of one other ecoregion.

Bioregions South Africa: Kalahari Duneveld (SVkd), W Eastern Kalahari Bushveld (SVk) (Savanna Biome); Upper Karoo (NKu) (Nama Karoo Biome); marginal in two other bioregions.

Assessment rationale: EOO = 390 575 km^2; AOO may be biased to arid regions of sandy soils; however, widespread in little-transformed regions used primarily for grazing of domestic livestock or conservation; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations and more precise assessment of EOO and AOO after taxonomic revision; protected in Kgalagadi Transfrontier Park (South Africa, Botswana), Namib-Naukluft National Park (Namibia).

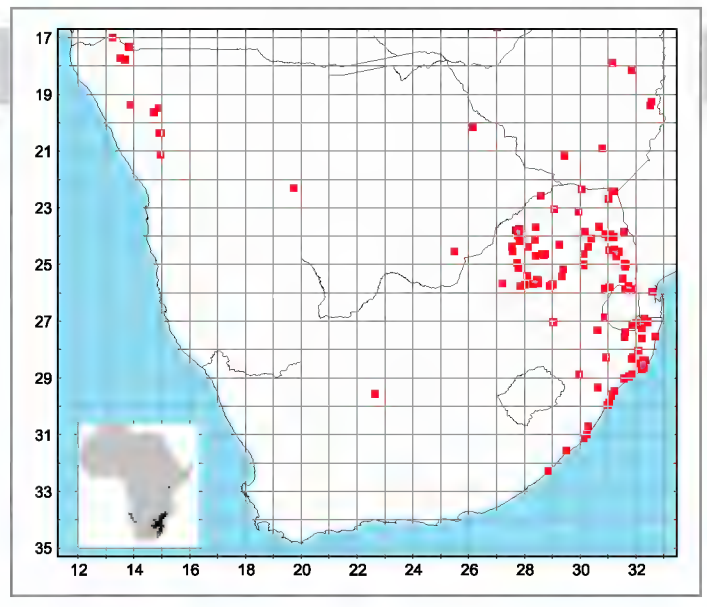
Hamonthophagus depressus

(Harold, 1871c)

= *Onthophagus laceratus* Gerstaecker *sensu* Péringuey, 1901
= *Onthophagus carteri* Blackburn, 1904
= *Onthophagus depressus* var. *marmoreus* d'Orbigny, 1904

Global: LC (see IUCN Red List – LC as *Onthophagus*)

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: As *Onthophagus depressus*: 'Caffraria' [SE South Africa], lectotype: 'SOUTH AFRICA: [Caffraria]'; *O. laceratus sensu* Péringuey: 'Natal (Durban, Malvern, Maritzburg)' [KwaZulu-Natal, South Africa]; *O. carteri*: 'N. S. Wales; Sydney' [Australia: accidental introduction]; var. *marmoreus*: Not stated.

Taxonomy: Accepted species recently transferred from *Onthophagus* Group 32 of d'Orbigny (1913); record for *O. laceratus* Gerstaecker *sensu* Péringuey, 1901, from 'Salem, Kuisip' [Namibia], would be *O. acutus* d'Orbigny, 1908; the record is marked, 'teste Boheman' [= witnessed by Boheman].

Distribution: Mostly known from sandy savanna and E coastal sands, southern Africa; NW and SE centres possibly separated by Kalahari deep sands; SW RSA outlier in Orange River Valley; Botswana, Namibia, South Africa, Mozambique, Malawi, Zimbabwe, Zambia, Angola, Democratic Republic of the Congo (DRC), Burundi, Tanzania; also recorded as a rarity on Kenyan coastal plain; accidental introduction into E Australia, SE USA, Madagascar, Mauritius.

Locality data (mean ± SD, range): Altitude: 701 ± 476, 0–1 762 m; annual rainfall: 676 ± 200, 190–1 198 mm; annual temperature (max. + min. /2): 20.1 ± 1.9, 15.5–24.4°C (N=128).

Habitat: No adequate quantitative data; across a post-mining vegetation gradient at Richards Bay: primarily in early succession shrubland (1.90), rare in grassland (0.03) and under shade in woodland (0.03); DBRU collection records from sand (12), sandy loam (5) in open shrub/woodland (10), pasture (4).

Food types: No adequate quantitative data; at Phalaborwa: only sampled to pig dung (3) not elephant or cattle dung (0); limited DBRU collection records to dung of cattle (14), horse (1), elephant (1), human/cattle mix (2).

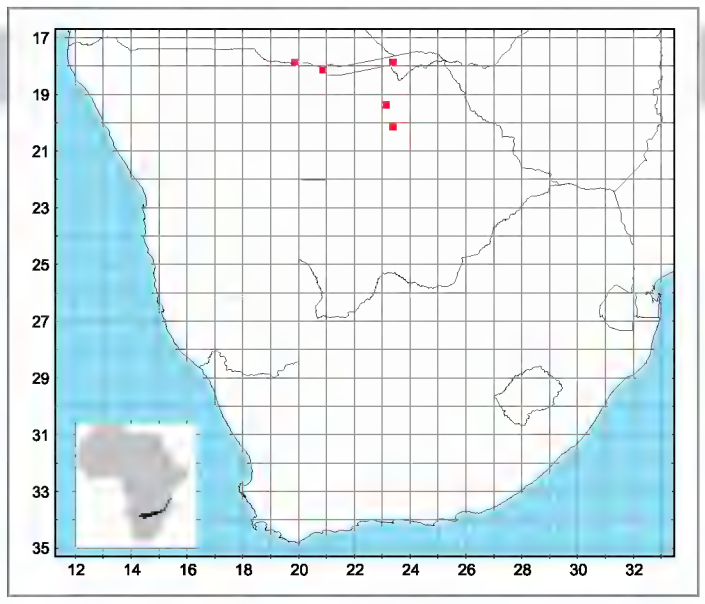
Temporal activity: Flight activity in darkness; recorded during most months of the year (Oct. to May; July, Aug.); attracted to light.

Ecoregions Namibia, Botswana, Zimbabwe, Mozambique: N Namibian Savanna Woodlands (AT1316), Kalaharia Xeric Savanna (AT1309), Kalahari Acacia-Baikiaea Woodlands (AT0709), Southern Miombo Woodlands (AT0719), Maputaland Coastal Forest Mosaic (AT0119).

Bioregions South Africa: Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome); Indian Ocean Coastal Belt Biome (CB); marginal in four other bioregions.

Assessment rationale: EOO = 669 355 km^2 (E African range underestimated); AOO may be restricted by soil and vegetation type specialisation, but data inconclusive; not recorded in the Kalahari despite an apparent bias to deep sands; usually recorded in low numbers but found across a wide area; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by better quantitative data on ecological associations; protected in Kruger National Park, uMkhuze Game Reserve (South Africa).



Hamonthophagus fallax

(d'Orbigny, 1913)

No synonyms

Global: DD

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'Afrique orientale allemande: Dar-es-Salam...; sud du Nyassa: Zomba dans la région du haut Chiré' [Dar es Salaam, Tanzania; Zomba in the region of the upper Shire River, Malawi], lectotype: 'MALAWI: [Nyassa Zomba haut Chiré]'.

Taxonomy: Accepted species recently transferred from *Onthophagus* Group 32 of d'Orbigny (1913).

Distribution: Dry to moist, hot, lowland savanna from S central to E Africa: Kenya, Tanzania, Burundi, Democratic Republic of the Congo (DRC), Malawi, Zambia, N Botswana, N Namibia; also cited from Angola; record from Eastern Cape, South Africa (Roggero et al. 2016), requires further validation.

Locality data (mean ± SD, range): Altitude: 884 ± 184, 492–1 075 m; annual rainfall: 666 ± 242, 443–1 108 mm; annual temperature (max. + min. /2): 22.5 ± 0.8, 21.4–23.9°C (N=7).

Habitat: No quantitative assessment; unknown.

Food types: No quantitative assessment; unknown.

Temporal activity: Diel flight periodicity unknown, but probably flies in darkness like other Group 32 species; active in summer rainy season (Nov. to Mar.).

Ecoregions Namibia, Botswana: Zambezian Baikiaea Woodlands (AT0726), N margins Zambezian and Mopane Woodlands (AT0725).

Assessment rationale: EOO = 327 565 km² (underestimated); range and ecological associations poorly known; S part of range may be associated with riverine systems and this needs to be investigated; currently assessed as Data Deficient (DD).

Conservation measures: Further investigation of range and ecological associations required before an assessment may be made of conservation status; protected in Liwonde National Park, Malawi.

Genus *Haroldius* Boucomont, 1914

Type species and designation: *Haroldius rugatulus* Boucomont, 1914, by subsequent designation (Arrow 1931).

Synonyms:
= *Cyclotrogus* Wasman, 1918: *Cyclotrogus heimi* Wasman, 1918, by original designation.
= *Ponerotrogus* Silvestri, 1924: *Ponerotrogus annandalei* Silvestri, 1924, by original designation.
= *Afroharoldius* Janssens, 1949: *Afroharoldius ennearthrus* Janssens, 1949, by original designation.
= *Formicdubius* Philips & Scholtz, 2000: Type species: *Formicdubius convexus* Philips & Scholtz, 2000, by original designation.

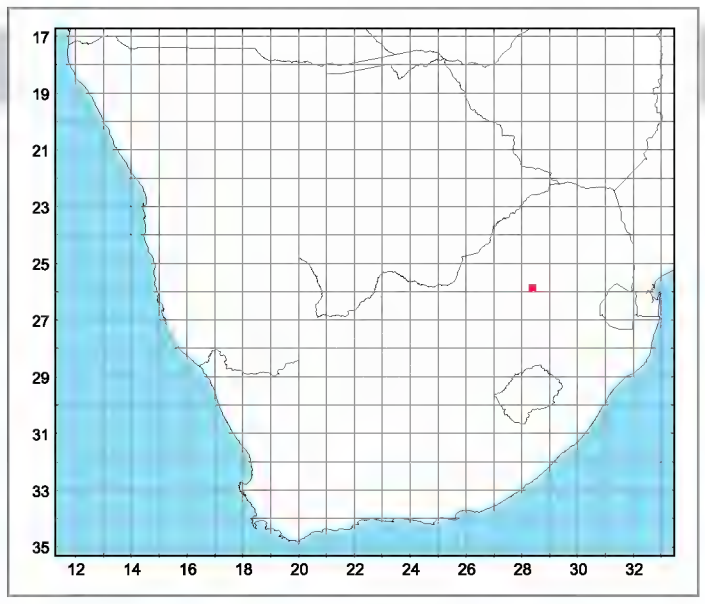
Last review: Entire genus and relatives considered by Krikken and Huijbrechts (2006), new Oriental species added subsequently.

The tribal level placement of *Haroldius* Boucomont, 1914, has been questioned. Although formerly placed in the Canthonini (Krikken & Huijbrechts 2006), the genus has most recently been assigned to the Onthophagini (Krell & Philips 2010; Philips 2016). However, the most recent molecular phylogeny (Tarasov & Dimitrov 2017) indicates affinities to basal Scarabaeinae currently classified with the Canthonini (Deltochilini) although bootstrap support varies from <50–59% using different methods.

Haroldius currently comprises 37 small-bodied species recorded in the Afrotropical (4) and Oriental regions (33). Various species have been cited as showing ant or termite associations including all those classified in the synonymous genera (Wasman 1918; Silvestri 1924; Janssens 1949; Philips & Scholtz 2000). However, as some species lack the trichomes (Krell & Philips 2010) that are indicators of myrmecophily, validity of the current generic membership of *Haroldius* requires further investigation.

Apparently, the four African species all possess trichomes, which are regions of setae associated with release of glandular secretions used to appease ants (Krell & Philips 2010). As some morphologically similar Oriental species also show ant associations, suggestions for revalidation of the past generic-level separation from Oriental *Haroldius* may or may not be justified.

A single *Haroldius* species has been recently recorded in association with ants at a single locality in South Africa (Philips & Scholtz 2000; Krell & Philips 2010). Ant or termite associations probably account for such rarity of collection and further African species may await discovery.



Haroldius convexus

(Philips & Scholtz, 2000)

= *Formicdubius convexus* Philips & Scholtz, 2000

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: *H. convexus*, *nom. nov.* for *Formicdubius convexus*: 'South Africa, Pretoria, The Willows, 25°45'S, 28°21'E'.

Taxonomy: Accepted species, but difficult to distinguish from the larger-bodied *H. leleupi* Janssens, 1953, described from Katanga [Lualaba Province], Democratic Republic of the Congo (DRC).

Distribution: Known only from the type locality in the suburbs of Pretoria [Tshwane], Gauteng, South Africa, within a region of moist, upland savanna.

Locality data (average): Altitude: 1 452 m; annual rainfall: 699 mm; annual temperature (max. + min. /2): 17.2°C (N=1).

Habitat: No quantitative assessment; type series of 16 individuals found under a stone together with ants (*Pheidole megacephala* (F.)).

Food types: No quantitative assessment; like all other African *Haroldius* species, apparently possesses trichomes (setae arranged singly or in clusters near the articulation between the abdomen and prothoracic disc), which would be indicative of ant association if involved in secretion of allomones.

Temporal activity: Diel periodicity unknown; recorded in the mid-summer rainy season (Jan.).

Bioregions South Africa: S edge of Central Bushveld (SVcb) (Savanna Biome).

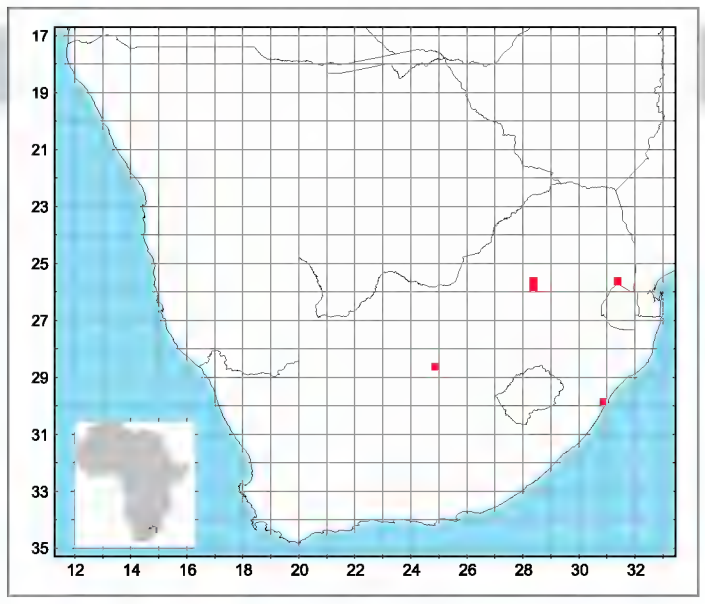
Assessment rationale: EOO not known; poorly represented in museum collections, probably owing to ecological specialisation and very small body size; although ecologically poorly known, found in association with ants like two of the other three known species (one with termites); possible host, *Pheidole megacephala*, is thought to be native to southern Africa, but is widespread across various vegetation types in various African countries; unknown if *H. convexus* shares this range; currently assessed as Data Deficient DD).

Conservation measures: It is necessary to resolve relationships with *H. leleupi* and mount a quantitative survey to determine EOO, AOO and ecological associations before an assessment of conservation status may be made; not currently known from any protected region.

Genus *Heteroclitopus* Péringuey, 1901

Type species and designation: *Heteroclitopus remipes* Péringuey, 1901, by monotypy.
Synonyms: None.
Last review: Entire genus reviewed by Branco (1991); new species added by Branco and Josso (2007).

Heteroclitopus Péringuey, 1901, currently comprises 10 poorly known species recorded in savanna and forest areas of the Afrotropical region. Rarity of collection despite widespread occurrence may indicate specialist habits although these are mostly unknown. *Heteroclitopus* are often sampled to light after nightfall. The single species described and recorded from E savanna of South Africa and Zimbabwe is the southernmost member of the genus. Péringuey (1901) speculates that it may be associated with termites.



Heteroclitopus remipes

Péringuey, 1901

No synonyms

Global: DD

| J | A | S | O | N | D | J | F | M | A | M | J |

Type localities: 'Natal (Durban), Southern Rhodesia (Upper Hanyani River)' [Durban, KwaZulu-Natal, South Africa; inexact, Zimbabwe].

Taxonomy: Accepted species.

Distribution: Scattered records suggest a widespread savanna and SE coastal distribution, but records are too few and/or inexact to determine the precise range; South Africa, Zimbabwe.

Locality data (mean ± SD, range): Altitude: 809 ± 597, 52–1 452 m; annual rainfall: 756 ± 209, 413–966 mm; annual temperature (max. + min. /2): 19.0 ± 1.4, 17.2–20.5°C (N=6).

Habitat: No quantitative assessment; unknown.

Food types: No quantitative assessment; unknown although Péringuey (1901) and Branco (1992) speculate on termite associations.

Temporal activity: Flight activity in darkness; seasonal activity unknown.

Bioregions South Africa: East Kalahari Bushveld (SVk), Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome); Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 42 635 km^2 (gross underestimate; South African range only); ecologically poorly known and rarely encountered, perhaps due to specialised association with termites; exact range uncertain; assessed as Data Deficient (DD).

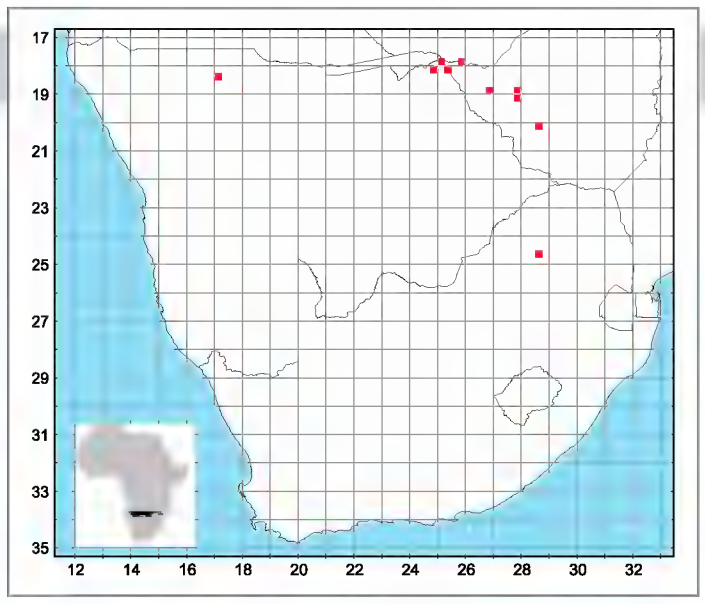
Conservation measures: To adequately assess conservation status, quantitative data on ecological associations is required, particularly data to determine whether or not it is ant- or termite-associated; protected in Dronfield Nature Reserve (South Africa).

Genus *Hyalonthophagus* Palestrini & Giacone, 1988

Type species and designation: *Onthophagus* (*Proagoderus*) *viridiceps* d'Orbigny, 1910, by original designation.
Synonyms: None.
Last review: Created as a subgenus of *Onthophagus* Latreille, 1802 (Palestrini & Giacone 1988), reviewed by Palestrini and Giacone (1989); one new species (Deschodt et al. 2019).

Although recently separated from *Proagoderus* van Lansberge, 1883, and described as a subgenus of *Onthophagus* Latreille, 1802, *Hyalonthophagus* Palestrini & Giacone, 1988 has been subsequently treated at either subgeneric (Palestrini & Giacone 1989) or generic level (Hanski & Cambefort 1991b). Although not formally raised to generic status by 2017, it was treated as a genus since it differs distinctly from other onthophagines. Subsequent to completion of this book, *Hyalonthophagus* has been formally raised to genus level with description of one new species (Deschodt et al. (2019); no species account, but see Preamble).

At the end of 2017, *Hyalonthophagus* comprised ten very closely related Afrotropical species distributed in the S, E and W within the drier or hotter savannas of the continent. Two described species, then, occurred within the savannas of Namibia, Botswana and South Africa: one in E savannas mainly in South Africa; one on the sands at the N and NE edge of the Kalahari (but see Preamble). Both are recorded with reasonable frequency and are therefore assessed as Least Concern (LC).



Hyalonthophagus alcyon

(Klug, 1855)

No synonyms

Global: DD (see IUCN Red List – DD)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Onthophagus alcyon*: 'Tette und Sena' [central Mozambique: Tete and Sena], lectotype: 'Tete and Sena'.

Taxonomy: Accepted species within a complex of very closely related taxa that are difficult to separate; limited sexual dimorphism (head); apparently characterised by metallic blue/black colouration.

Distribution: Patchy records from savanna of southern central Africa: N and NE edges of S Kalahari and Zambezi River Valley; Mozambique, N South Africa, W Zimbabwe, N Botswana, S Angola; citations from Kenya, Tanzania require validation.

Locality data (mean ± SD, range): Altitude: 938 ± 315, 61–1 229 m; annual rainfall: 635 ± 95, 472–813 mm; annual temperature (max. + min. /2): 21.9 ± 1.7, 19.6–25.7°C (N=12).

Habitat: No quantitative assessment; suspected to be a deep sand specialist, but not well supported by available data; limited DBRU collection records on sand (2), sandy loam (2), sandy clay loam (1) in grassland (1), open woodland (3).

Food types: No quantitative assessment; DBRU collection records biased to dung of monogastric herbivores (elephant, 8) compared to ruminant herbivores (cattle, 3).

Temporal activity: Diurnal flight activity during the summer rainy season (Nov. to Feb.).

Ecoregions Namibia, Botswana, Zimbabwe: Angolan Mopane Woodlands (AT0702), Zambezian Baikiaea Woodlands (AT0726), Zambezian and Mopane Woodlands (AT0725).

Bioregions South Africa: Central Bushveld (SVcb) (Savanna Biome).

Assessment rationale: EOO = 474 810 km^2; EOO a gross estimate based on limited available data; poorly known and possibly confused with other species; AOO and population density may be influenced by soil (sand) and dung type specialisation (dung of monogastric herbivores and their occurrence), but quantitative data is required in support; currently assessed as Data Deficient (DD).

Conservation measures: Assessment of conservation would be improved by survey and accurate identification to determine full EOO and by quantitative data on ecological associations to determine AOO; protected in several national parks: Chobe (Botswana), Hwange (Zimbabwe), Bicuar (Angola).

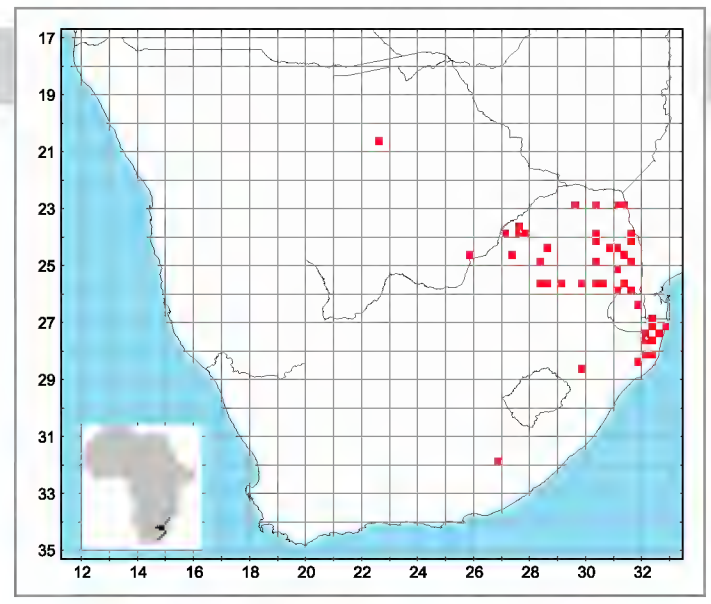
Hyalonthophagus alcyonides

(d'Orbigny, 1913)

= *Oniticellus splendens* Wallengren, 1881
= *Onthophagus (Proagoderus) alcyon* var. *viridiceps* d'Orbigny, 1902
= *Onthophagus (Proagoderus) alcyon* var. *virens* d'Orbigny, 1902

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: as *Onthophagus alcyonides*: 'Lac Ngami.....; Transvaal: Shilouvane près de Leydsdorp....; Natal: Ladysmith....; Colonie du Cap: Port-Elizabeth' [Botswana: Lake Ngami; South Africa: Shilouvane, Ladysmith, Port Elizabeth], lectotype: 'Transvaal: Shilouvane'; *O. splendens*: 'Transvaalia' [South Africa]; var. *viridiceps* and var. *virens*: 'Mozambique'.

Taxonomy: Accepted species within a complex of very closely related taxa that are difficult to separate; limited sexual dimorphism (head); metallic colouration varies from cupreous to green; status of Wallengren synonym requires further study.

Distribution: Mostly moist savanna centred on NE South Africa with scattered outlier records in Botswana, central and N Mozambique, SE South Africa.

Locality data (mean ± SD, range): Altitude: 576 ± 473, 0–1 628 m; annual rainfall: 694 ± 177, 414–1 220 mm; annual temperature (max. + min. /2): 20.9 ± 2.1, 15.1–25.2°C (N=62).

Habitat: In Gauteng bushveld: strong bias to deep sand (134) compared to sandy clay loam (3) and to open woodland (107) compared to shaded thicket (5) or grassland (25) (wrongly cited as *H. alcedo* d'Orbigny, 1913); in uMkhuze Game Reserve: no consistent soil bias, sand (5.4), sand on clay (3.2), sandy clay loam (2.5), clay (4.9); DBRU collection records suggest a bias to finer-grained soils, sand (6), sandy loam (6), sandy clay loam (12), clay (1) in grassland/pasture (8), open shrub/woodland (16), forest/thickets (3).

Food types: In Gauteng bushveld: strong bias to omnivore dung (pig: 75) compared to herbivore dung (horse: 11; cattle: 6) (wrongly cited as *H. alcedo* d'Orbigny, 1913); DBRU collection records from dung of cattle (13), buffalo (1), wildebeest (1), elephant (8), rhinoceros (3), donkey (1), baboon (2), human/cattle mix (1).

Temporal activity: Diurnal flight activity during the summer rainy season (Oct. to Mar.).

Ecoregions Botswana: Kalahari Acacia-Baikiaea Woodlands (AT0709).

Bioregions South Africa: Centred on Central Bushveld (SVcb), Lowveld (SVl), moister edges of Mopane (SVmp) (Savanna Biome); also N margins of two other bioregions with a few scattered records in Sub-Escarpment Grassland (Gs) (Grassland Biome).

Assessment rationale: EOO = 232 285 km^2; widespread in moist woody savanna of NE South Africa in both farm rangeland and reserves; data suggest that clearance of woodland would reduce population density; however, currently assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data to resolve conflicting results on soil associations; protected in uMkhuze Game Reserve, Kruger National Park (South Africa).

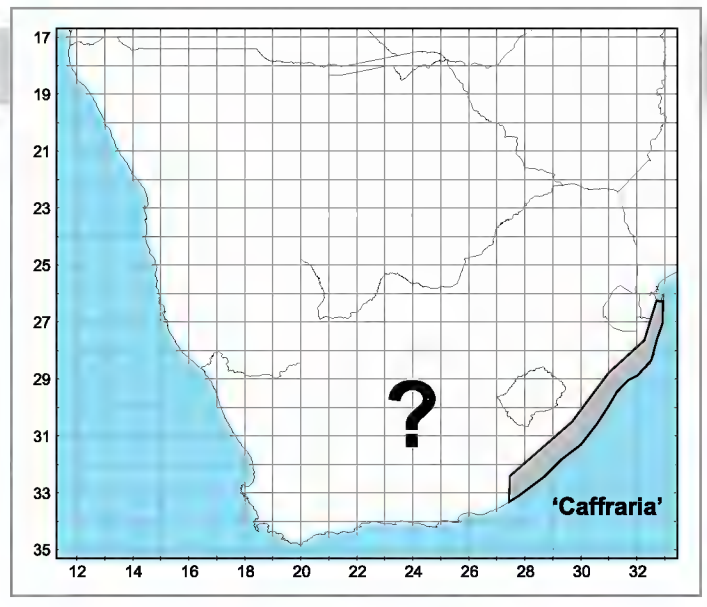
Genus *Kurtops* Roggero, Barbero & Palestrini, 2016

Type species and designation: *Onthophagus signatus* Fahraeus, 1857, by original designation.
Synonyms: None.
Last review: Genus created and reviewed by Roggero et al. (2016).

Kurtops Roggero, Barbero & Palestrini, 2016, was recently created to accommodate the species comprising Group 21 (d'Orbigny 1913) of *Onthophagus* Latreille, 1802. Strong evidence is presented by Roggero et al. (2016) to support this decision. *Kurtops* currently comprises three endemic Afrotropical species with distributions centred in southern Africa. The two better known species are common on sandy soils in the Kalahari or the Kalahari and E coast. The third is extremely poorly known.

Kurtops caffrarius

(d'Orbigny, 1902)



No synonyms

Global: DD
Endemic: RSA

| J | A | S | O | N | D | J | F | M | A | M | J |

Type locality: 'Caffrérie' [inexact, 'Caffraria'; somewhere in southern Africa].

Taxonomy: Accepted species known by single holotype specimen; formerly classified in *Onthophagus* Group 21 and recently transferred to the new genus, *Kurtops* Roggero, Barbero & Palestrini, 2016; one unlabelled specimen seen in Ditsong Museum.

Distribution: No precise known locality; type locality of 'Caffraria' variously used by different collectors and authors to refer to SE Africa or even the entire subcontinent of southern Africa.

Locality data: None available.

Habitat: Not known.

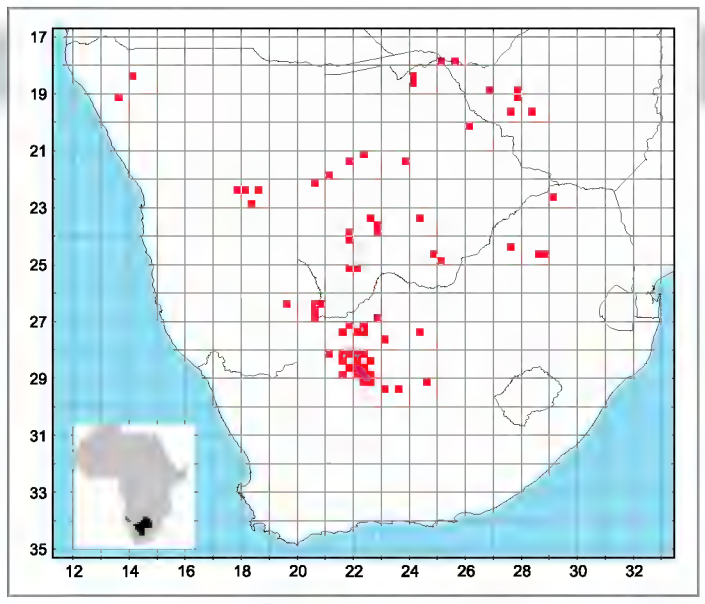
Food types: Not known.

Temporal activity: Diel flight periodicity and seasonal activity unknown.

Bioregions South Africa: Unknown.

Assessment rationale: EOO unknown; as a very close relative of the Kalahari-centred *K. quadraticeps* (Harold, 1867), *K. caffrarius* might be expected to show similar specialist habitat associations on deep sand in open shrub/grassland, but there is no support for this hypothesis; known by extremely few old museum records; given the absence of precise locality data and lack of ecological data, assessed as Data Deficient (DD); however, paucity of records presumably indicates specialist association and/or highly restricted range.

Conservation measures: Impossible to recommend any conservation measures considering the paucity of distribution and ecological data; no obvious focal area for a survey to rediscover this species; occurrence within the shaded area on the map considered unlikely; occurrence in large area around question mark, possibly, more likely.



Kurtops quadraticeps

(Harold, 1867c)

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Freistaat Oranje' [Free State, South Africa].

Taxonomy: Accepted species formerly classified in *Onthophagus* Group 21 and recently transferred to the new genus, *Kurtops* Roggero, Barbero & Palestrini, 2016.

Distribution: Arid to dry deep sands of the Kalahari, E Kalahari outliers and deep sands in Kaokoveld; South Africa, Botswana, Namibia, Zimbabwe.

Locality data (mean ± SD, range): Altitude: 1 079 ± 158, 703–1 684 m; annual rainfall: 321 ± 122, 157–659 mm; annual temperature (max. + min. /2): 19.8 ± 1.2, 16.3–23.1°C (N=115).

Habitat: No quantitative assessment; on deep sand in Botswana: much more abundant in the open shrub/grassland of the arid SW (1 242) than the moister NE (46); DBRU collection records from sand (23), sandy loam (4), sandy clay loam (1) in open woodland (5), scrub/shrubland (14), grassland (5).

Food types: On deep sand in Botswana: strong bias to omnivore dung (pig: 794), but also attracted to herbivore dung types (elephant: 207, cattle: 97, sheep: 184), poorly attracted to carrion (chicken livers: 3); DBRU collection records from the dung of cattle (22), buffalo (1), waterbuck (1), elephant (1), horse (1), donkey (2).

Temporal activity: Flight activity in darkness during the summer rainy season (Nov. to Apr.); attracted to light.

Ecoregions Namibia, Botswana, Zimbabwe: N Namibian Savanna Woodlands (AT1316), Kalahari Xeric Savanna (AT1309), Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian Baikiaea Woodlands (AT0726), NW Zambezian and Mopane Woodlands (AT0725).

Bioregions South Africa: Kalahari Duneveld (SVkd), Eastern Kalahari Bushveld (SVk), sand outliers: Central Bushveld (SVcb), Mopane (SVl), (Savanna Biome); extreme N margins Nama Karoo Biome.

Assessment rationale: EOO = 799 195 km²; observations suggest that the AOO is restricted by soil specialisation although deep sand covers > 80% of the widespread EOO; range is little transformed, particularly in the SW, which is used primarily for the grazing of domestic livestock to whose dung it is readily attracted despite a bias to omnivore dung; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on soil and vegetation associations; protected in Central Kalahari Game Reserve and Kgalagadi Transfrontier Park (Botswana, South Africa).

Kurtops signatus

(Fahraeus, 1857)

= *Onthophagus junodi* d'Orbigny, 1902

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *K. signatus*: 'prope fluvium Limpopo' [close to Limpopo River, southern Africa]; *O. junodi*: 'Mozambique: district de Delagoa..., Delagoa-Bay' [Maputo, Mozambique].

Taxonomy: Accepted species formerly classified in *Onthophagus* Group 21 and recently transferred to the new genus, *Kurtops* Roggero, Barbero & Palestrini, 2016; synonymy of *O. junodi* should be re-examined; elytral colour change from entirely cream to increasing amounts of melanic patternation, currently considered to represent intraspecific variation.

Distribution: Widespread on sandy soils in dry inland and moist SE coastal savanna of southern Africa: Angola, Namibia, Botswana, South Africa, Zimbabwe, Mozambique.

Locality data (mean ± SD, range): Altitude: 935 ± 347, 0–1 958 m; annual rainfall: 362 ± 193, 133–971 mm; annual temperature (max. + min. /2): 19.8 ± 1.8, 14.3–23.7°C (N=293).

Habitat: In uMkhuze Game Reserve: extreme bias to sand (132.0) compared to sand over clay (3.6), sandy clay loam (0.1), clay (0.3); supported in Gauteng bushveld: sand (74), sandy clay loam (1) with a bias to open woodland (50) and grassland (25), not in shaded thickets (0); supported by DBRU collection records on sand (33), sandy loam (13) in grassland/pasture (10), scrub/shrubland (13), open woodland (22).

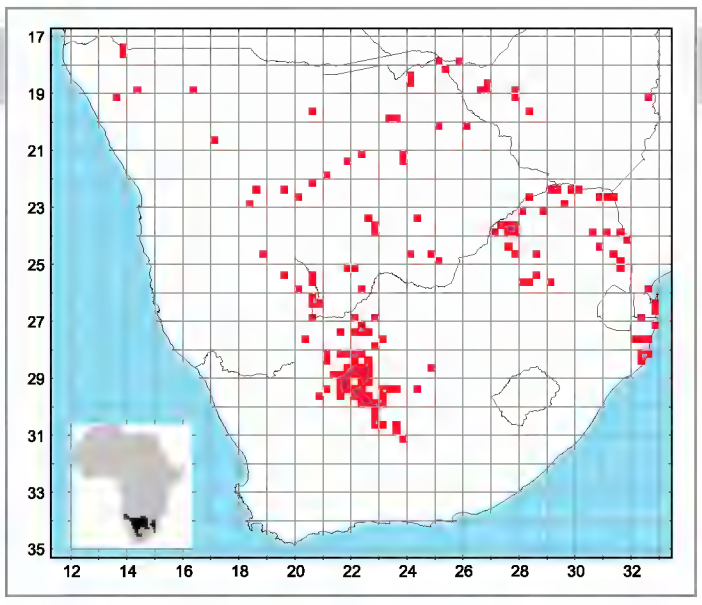
Food types: In Botswana: attracted in abundance to various dung types: pig (3 727), elephant (1 705), cattle (960), sheep (2 221) and rarely to carrion (46); at Phalaborwa: similar bias to dung of pig (238), but more to cattle (160) than elephant (57); DBRU collection records on various dung types: cattle (32), wildebeest (1), impala (1), elephant (6), rhinoceros (1), zebra (1), horse (1), donkey (4), human (2), human/cattle mix (1)

Temporal activity: Diurnal flight activity during most months of the year (Aug., Oct. to May); but, in Gauteng bushveld: primarily active early in the rainy season (Oct. to Dec.) tailing off into later summer (Jan., Feb.); at Phalaborwa: moderately affected by weather conditions: warm cloudy day following light rainfall (148), hot dry day (104), warm day soon after very heavy rainfall (204).

Ecoregions Namibia, Botswana, Zimbabwe, Mozambique: N Namibian Savanna Woodlands (AT1316), Kalahari Xeric Savanna (AT1309), Angolan Mopane Woodlands (AT0702), Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian Baikiaea Woodlands (AT0726), Zambezian and Mopane Woodlands (AT0725), Maputaland Coastal Forest Mosaic (AT0119).

Bioregions South Africa: N Bushmanland (NKb), N Upper Karoo (NKu) (Nama Karoo Biome); Kalahari Duneveld (SVkd), Eastern Kalahari Bushveld (SVk), Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome); N Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 1 133 835 km² (underestimated); AOO limited by occurrence of deep sands and other particularly sandy soils, but these are widespread in southern Africa; recorded in abundance over a wide area on a variety of dung types; occurs in grassland, but bias to tree savanna suggests population density might be adversely affected



Melanic elytra

Pale elytra

Kurtops signatus (continued)

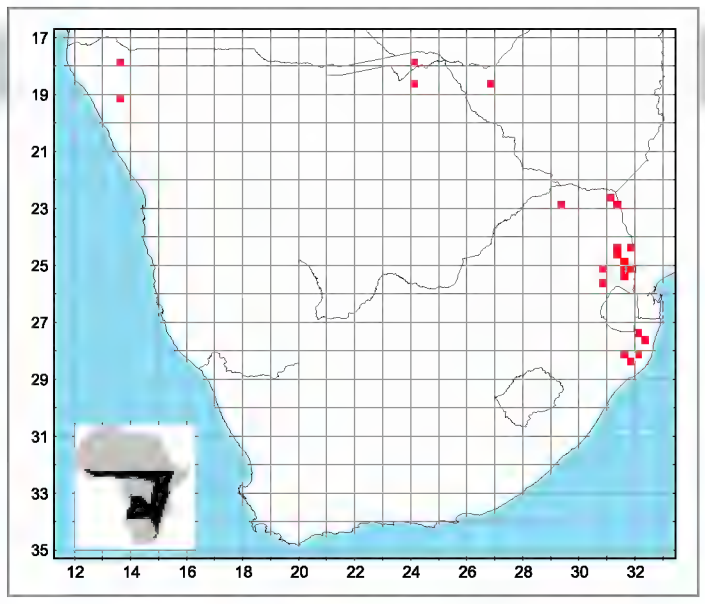
by clearance of woodland; transformation in NE range in South Africa: 0–58% (SVl), 2–49% (SVcb), 0–20% (SVmp); however, widespread with SW range in little-transformed farmland used primarily for grazing of domestic livestock; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by more detailed data on effects of shrubland and woodland clearance; protected in various national parks, including: Kruger (South Africa), Hwange (Zimbabwe), Chobe (Botswana).

Genus *Milichus* Péringuey, 1901

Type species and designation: *Onthophagus apicalis* Fahraeus, 1857, by monotypy.
Synonyms: None.
Last review: Entire genus reviewed by Cambefort (1996b).

Milichus Péringuey, 1901, currently comprises 15 species recorded from dry to moist savannas and forests in the lowlands to uplands of the Afrotropical region. Two species have been recorded in the region encompassing South Africa, Botswana and Namibia. One, recorded primarily from monogastric herbivore dung, occurs in dry to moist savanna throughout Africa. The other from the E coast of South Africa remains unnamed so no species account is presented.



Milichus apicalis

(Fahraeus, 1857)

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Onthophagus apicalis*: 'in terra Natalensi' [KwaZulu-Natal, South Africa].

Taxonomy: Currently accepted as a single extremely widely distributed species; minor sexual dimorphism (prothoracic disc).

Distribution: Widespread in dry to moist African savanna, but, now, mostly localised in game reserves owing to dung specialisation: South Africa, Zimbabwe, Botswana, Namibia, Kenya, Côte d'Ivoire; also cited from Angola, Mozambique, Somalia, Ethiopia, Uganda, Rwanda, Burundi, Democratic Republic of the Congo (DRC), Gabon, Chad, Nigeria, Guinea (Conakry).

Locality data (mean ± SD, range): Altitude: 509 ± 316, 55–1 227 m; annual rainfall: 657 ± 175, 171–1 121 mm; annual temperature (max. + min. /2): 21.6 ± 1.9, 16.8–24.4°C (N=32).

Habitat: In uMkhuze Game Reserve: strong bias to finer-grained soils: sand (1.6), sand on clay (10.0), sandy clay loam (29.4), clay (2.8) with a 63% bias to woodland (N=407); at South African Wildlife College (Kruger National Park) and adjacent communal rangeland: bias to finer-grained gabbro-derived (53.0, 51.9) rather than coarser-grained granite-derived soils (30.7, 29.8); DBRU collection records on sand (1), sandy loam (5), clay (1) in shrubland (2), open woodland (5), shaded thicket (1).

Food types: On deep sand in NE Botswana: sampled only to elephant dung (18), zero (0) on dung of omnivores (pig), ruminant herbivores (cattle, sheep) and carrion (chicken livers); at Phalaborwa: extreme bias to elephant dung (40) compared to pig (2) and cattle dung (2); DBRU collection records primarily from dung of monogastric herbivores: elephant (8), rhinoceros (2), but also cattle dung (2).

Temporal activity: Flight activity in darkness during the summer rainy season (Oct. to Mar.); at Phalaborwa: primarily active in warm weather after heavy rainfall (31) rather than in hot, dry weather (5) or warm weather after light rainfall (8).

Ecoregions Namibia, Botswana, Zimbabwe: N Namibian Savanna Woodlands (AT1316), Zambezian and Mopane Woodlands (AT0725).

Bioregions South Africa: Lowveld (SVl), Mopane (SVmp) (Savanna Biome).

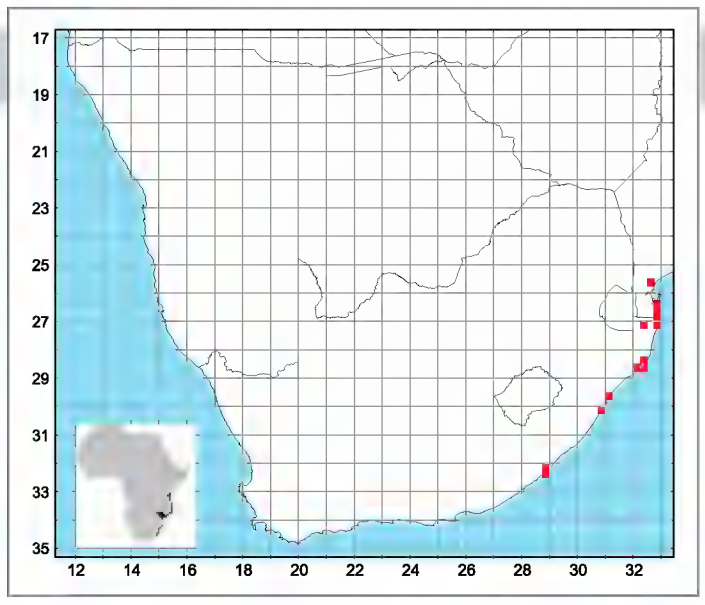
Assessment rationale: EOO = 7 382 875 km² (gross estimate); AOO much smaller due to association with the dung of indigenous monogastric herbivores whose ranges have now mostly contracted into game reserves, hence the fragmented pattern on the map of southern Africa; AOO and population density probably also influenced by soil and vegetation bias; however, owing to extremely wide range and ample protection in reserves, currently assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on vegetation associations and possible effects of woodland clearance; conservation status clearly linked to continuing protection of large monogastric herbivores, particularly, elephant and rhinoceros; protected in various national parks including Kruger (South Africa), Chobe (Botswana), Tsavo East (Kenya).

Genus *Mimonthophagus* Balthasar, 1963b

Type species and designation: *Onthophagus apicehirtus* d'Orbigny, 1915, by original designation.
Synonyms: None.
Last review: Entire genus reviewed by Moretto (2009).

Mimonthophagus Balthasar, 1963b, currently comprises eight species with Afrotropical (7) and Madagascar (1) distributions. The three species of S and S to E Africa are centred in savannas and this may also be true of four species centred in W central Africa although available locality data is inexact. Of the three species found in Botswana and/or South Africa, one appears to be a specialist on E coastal sands with a range extending into the E tropics. The other two may be associated primarily with elephant dung on sandy soils although current evidence is weak. One is found only at the NE edge of the Kalahari whereas the other has a range extending into the E tropics.



Mimonthophagus ambiguus

(Péringuey, 1901)

= *Onthophagus hinnulus* Klug, 1832, *sensu* Gerstaecker, 1873
= *Caccobius bicornutus* Frey, 1955

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Onthophagus ambiguus*: 'Natal (Isipongo)' [Isipingo, KwaZulu-Natal, South Africa]; *O. hinnulus sensu* Gerstaecker: 'Insel Sansibar' [Zanzibar, Tanzania]; *C. bicornutus*: 'Sansibar.....Tanganyika Mhonda' [NE Tanzania].

Taxonomy: Accepted species; sexually dimorphic (head, prothoracic disc).

Distribution: E coastal sands from The Haven, South Africa, to at least, Malindi, Kenya; also up Zambezi River Valley system to Rekommetjie/ Lake Malawi shores: South Africa, Mozambique, Zimbabwe, Tanzania, Kenya; also cited from Malawi.

Locality data (mean ± SD, range): Altitude: 34 ± 100, 0–541 m; annual rainfall: 857 ± 134, 681–1 275 mm; annual temperature (max. + min. /2): 22.1 ± 1.3, 18.9–24.6°C (N=31).

Habitat: No quantitative data for soil association; on deep sand in Maputo Special Reserve: strong bias to grassland on fossil lagoons (96.0) compared to sand forest patches (large, 4.7; medium, 23.0; small, 7.9) and cooler coastal dune forest (1.8); severely limited DBRU collection records on sand (3) in pasture (1), open woodland (1).

Food types: No quantitative data: severely limited DBRU collection records on dung of cattle (3); sampled to pig dung.

Temporal activity: Flight activity in darkness (18:00–20:00) during the summer rainy season (Nov. to May).

Ecoregions Mozambique: Maputaland Coastal Forest Mosaic (AT0119), Southern Zanzibar-Inhambane Coastal Forest Mosaic (AT0128).

Bioregions South Africa: Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 298 230 km^2; range suggests a sand specialist although quantitative support is currently lacking; occurs in warm forested areas although a strong bias to bias to open situations suggests forest clearance would not be detrimental to population density; widespread along the E coast and found in abundance in coastal reserves; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on soil and food associations; protected in iSimangaliso Wetland Park (World Heritage Site) (South Africa), Maputo Special Reserve (Mozambique).

Mimonthophagus anomalus

(Klug, 1855)

= *Onthophagus moestus* Fahraeus, 1857
= *Onthophagus calvus* d'Orbigny, 1904
= *Onthophagus julianae* Paulian, 1937
= *Onthophagus muripedis* Frey, 1975b

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Onthophagus anomalus*: 'Sena' [central Mozambique]; *O. moestus*: 'in terra Natalensi' [KwaZulu-Natal, South Africa]; *O. calvus*: 'Boran Galla: Haouacio' [Ethiopia]; *O. julianae*: 'Afrique: Uganda'; *O. muripedis*: 'Rhodesien: Wankie, Kariba, Dett, Kenmaur; Transvaal, Krueger Nationalpark: Pundamilia; Botswanaland: Chobe; Moçambique: Gorongosa' [Zimbabwe, South Africa, Botswana, Mozambique].

Taxonomy: Accepted species; minor sexual dimorphism (fore tibiae).

Distribution: Widespread across savanna from S to NE Africa, but shows patchy occurrence centred mainly on game reserves: NE South Africa, Mozambique, Zimbabwe, Botswana, N Namibia, Angola, Tanzania, Uganda, Ethiopia; also cited from Kenya.

Locality data (mean ± SD, range): Altitude: 730 ± 350, 59–1 247 m; annual rainfall: 647 ± 145, 466–1 136 mm; annual temperature (max. + min. /2): 22.7 ± 1.5, 19.3–25.7°C (N=22).

Habitat: No quantitative data; DBRU collection records primarily from game reserves or protected areas on sand (1), sandy loam (3), sandy clay loam (1), clay (1) in grassland (2), open woodland (4).

Food types: In Botswana: strong bias to omnivore dung (pig: 1 061) compared to other dung types (elephant: 115; cattle: 19; sheep: 245) and carrion (chicken livers: 7); however, DBRU collection records primarily from dung of elephant (10), also zebra (1), cattle (2).

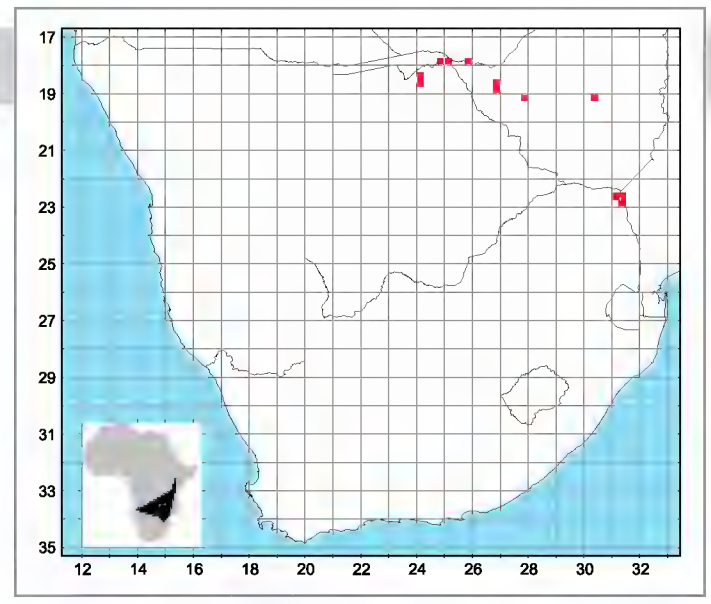
Temporal activity: Flight activity in darkness during the summer rainy season (Nov. to Apr.); attracted to light.

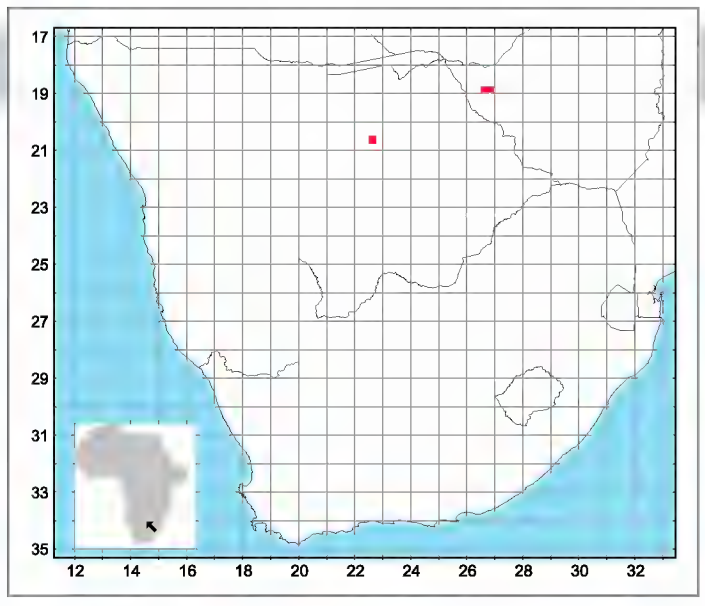
Ecoregions Botswana, Zimbabwe: Zambezian and Mopane Woodlands (AT0725).

Bioregions South Africa: Mopane (SVmp) (Savanna Biome).

Assessment rationale: EOO = 2 658 380 km² (gross estimate); despite a measured bias to omnivore dung, recently found primarily on elephant dung in game reserves (88.2% of available S records, N=15 out of 17); despite this apparent range contraction to a much smaller AOO, it is found in various reserves across a very large EOO; therefore, currently, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on habitat associations; protected in various national parks including: Kruger (South Africa), Hwange (Zimbabwe), Chobe (Botswana), Bicuar (Angola), Manyara (Tanzania).





Mimonthophagus limbibasis

(d'Orbigny, 1905)

No synonyms

Global: DD (see IUCN Red List – NT)

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Onthophagus limbibasis*: 'Lac Ngami' [Lake Ngami, N Botswana].

Taxonomy: Accepted species.

Distribution: Only known from savanna woodland on the sand/sandy loam soil mosaic at the northeast edge of the S Kalahari: Botswana, Zimbabwe.

Locality data (mean ± SD, range): Altitude: 1 044 ± 104, 924–1 106 m; annual rainfall: 540 ± 109, 414–608 mm; annual temperature (max. + min. /2): 21.6 ± 0.7, 21.1–22.4°C (N=3).

Habitat: No quantitative assessment; limited DBRU collection records from sandy loam (2) in open woodland (2).

Food types: No quantitative assessment; limited DBRU collection records from the dung of monogastric herbivores (elephant, 3).

Temporal activity: Diel flight periodicity unknown, but possibly flies in darkness like other *Mimonthophagus* species; recorded during the summer rainy season (Nov., Feb.).

Ecoregions Botswana, Zimbabwe: Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian Baikiaea Woodlands (AT0726).

Assessment rationale: EOO = 2 790 km^2 (possibly underestimated); poorly known species represented by few individuals in museum collections; on the basis of apparent rarity and possible ecological specialisation, particularly to the dung of range-restricted elephant, this species has been assessed as Near Threatened (NT) on the IUCN Red List; however, assessed here as Data Deficient (DD).

Conservation measures: To assess conservation status, a quantitative survey of N Botswana, W Zimbabwe and surrounding regions is required to determine the EOO, AOO and ecological associations; in particular, the possibility of finer-grained soil, woodland and elephant dung specialisation needs to be investigated; protected in Hwange National Park, Zimbabwe.

Genus *Onthophagus* Latreille, 1802

Type species and designation: *Scarabaeus taurus* Schreber, 1759, by monotypy.
Synonyms: = *Psilax* Erichson, 1848: Type species: *Onthophagus pronus* Erichson, 1848, by monotypy.
= *Monapus* Erichson, 1848: Type species: none verified.
Last review: Afrotropical members of genus reviewed by d'Orbigny (1913); subsequent additions of 239 new Afrotropical species currently classified in *Onthophagus*; some subsequent synonymies and various changes in status as regards raising of species groups to subgenera within *Onthophagus* or separation from *Onthophagus* at generic level (see below).

The long-established genus, *Onthophagus* Latreille, 1802, is represented globally within tropical, warm temperate and winter rainfall regions with limited penetration into temperate climates. It is currently represented by approximately 2 145 species, although numbers frequently change because of the addition of new species, subtraction of synonyms or subtraction of species due to raising of species groups or subgenera to generic level. Numbers of regional species cited here are essentially estimates owing to the frequency of additions and subtractions (Neotropical: 92; Nearctic: 76; Palaearctic: 192; Oriental: 666 (reduced by ~90 species after *Parascatonomus* Paulian, 1932, was raised from subgeneric to generic level (Ochi et al. 2012)); Afrotropical: 796; Madagascar: 4; Australia: 201; New Guinea: 118).

Of the synonyms recently cited for the genus (Smith 2009), only two are cited above. Other names have been revalidated at subgeneric level by Moretto (2009) (*Gonocyphus* van Lansberge, 1885b); have become a synonym of *Proagoderus* van Lansberge, 1883 (*Tauronthophagus* Shipp, 1895c); or, a possible synonym of *Parascatonomus* (*Chalcoderus* Erichson, 1848). If *Chalcoderus* was awarded the status of *nomen oblitum* (=forgotten name) (Palestrini 1982), it would become a synonym of *Paracatonomus* due to affiliations shown by the *Chalcoderus* type species, *Onthophagus maculatus* (Fabricius, 1801) (see Group 15 notes).

The review of d'Orbigny (1913) examined the entire membership of *Onthophagus* in the Afrotropical region. Four subgenera were recognised. All have subsequently been raised to generic level (*Proagoderus*; *Phalops* Erichson, 1847b; *Diastellopalpus* van Lansberge, 1886; *Onthophagus s. str.*). A total of 32 species groups were recognised within *Onthophagus s. str.* For those Afrotropical groups that remain classified within *Onthophagus*, many subsequent papers by 20 different authors have added 239 new species to those described during or before 1913. The process of revision continues and it is likely that all of d'Orbigny's 32 core groups will ultimately be raised to subgeneric or generic level. Some have already received formal subgeneric names or have been extracted to other genera.

The alpha taxonomy of southern African *Onthophagus* remains incomplete and requires much revision.

(1) No accounts were prepared for a total of 41 currently valid species described from South Africa, Botswana or Namibia as the names could not be reliably matched to reference material.

(2) No accounts were prepared for another eight species described from elsewhere since claimed records from southern Africa could not be verified.

(3) Many species from South Africa, Botswana and Namibia could not be included as names were unavailable or could not be validated even, in some cases, for species that were well represented in collections with supporting ecological data.

(4) Undoubtedly, a number of species remain undescribed; some current valid species names are synonyms; some synonyms deserve revalidation; whereas some have been synonymised with the wrong species.

(5) The 78 species accounts presented, here, may represent only 50–60% of the true diversity of *Onthophagus* in South Africa, Botswana and Namibia. However, even some of the species names included in the accounts require validation or revision.

The group structure proposed by d'Orbigny (1913) is used as a guide to representation by *Onthophagus* and former *Onthophagus* in South Africa, Botswana and Namibia on the understanding that it represents a stage in the revision of the species complexes.

Group 1: See four probable ant or termite-associated genera (*Pseudosaproecius* Balthasar, 1941b; *Eusaproecius* Branco, 1989; *Cambefortius* Branco, 1989) including one represented in southern Africa: *Stiptopodius* Harold, 1871b (but not validated).

Group 2: Four validated widespread species; ranges into E tropics.
Group 3: Represented in southern Africa, but no validated species.
Group 4: One validated highland, endemic; South African species.
Group 5: Subgenera, *Gonocyphus* van Lansberge, 1885b, and *Afrostrandius* Moretto, 2009; in the S: one *Afrostrandius* on monogastric herbivore dung in savanna; ranging into E tropics.
Group 6: See genus, *Mimonthophagus* Balthasar, 1963a.
Group 7: Subgenera, *Eremonthophagus* Zunino, 1979, and *Bicornonthophagus* Tagliaferri & Moretto, 2012: accounts for seven widespread (1), southern African (1) or SE African (5) taxa.
Group 8: See genus, *Euonthophagus* Balthasar, 1959.
Group 9: Four validated species endemic to South Africa.
Group 10: Two southern African (1) or widespread (1) taxa.
Group 11: Kleptocoprid species; accounts for seven widespread (1), southern African (4), or South African endemic (2) taxa.
Group 12: Subgenus, *Trichonthophagus* Zunino, 1979: possibly kleptocoprid on *Heliocopris* species; accounts for seven widespread (1) or southern African (6) taxa.
Group 13: Represented in southern Africa but no validated species; some species transferred to genera, *Digitonthophagus* Balthasar, 1959, and *Phalops* Erichson, 1847b.
Group 14: Represented in South Africa and Namibia by two species that have been validated and transferred to the new genus, *Jossonthophagus* Dierkens, Moretto & Génier, 2017, only after submission of this book, so no species accounts.
Group 15: One Group 15 member (*Onthophagus maculatus*) now in genus, *Parascatonomus* Paulian 1932; one southern African group member (*Onthophagus graphicus* Wallengren, 1881) remains classified in *Onthophagus*; *O. graphicus* is a carrion species in southern African savannas, ranging into the E tropics.
Group 16: Accounts for seven species endemic to South Africa (3), southern Africa (3), or widespread to E tropics (1).
Group 17: Accounts for four species endemic to South Africa (3) or southern Africa (1).
Group 18: Carrion-associated; accounts for five species endemic to South Africa (3), Namibia (1), or widespread to E tropics (1).
Group 19: Carrion-associated; accounts for five taxa widespread to E tropics (2) or endemic to southern (1) or South Africa (2).
Group 20: Accounts for two SW Arid (1) or Kalahari (1) species.
Group 21: See genus, *Kurtops* Roggero, Barbero & Palestrini, 2016.
Group 22: Account for one Kalahari-centred species.
Group 23: Accounts for six species widespread in the tropics (2) or endemic to South Africa (4).
Group 24: Accounts for five species widespread to E tropics (1) or centred in southern Africa (4) (one now transferred to the new genus, *Tiaronthophagus* Roggero, Moretto, Palestrini & Barbero, 2019).
Group 25: Palaearctic species group.
Group 26: E African montane species group.
Group 27: Removed from Afrotropical fauna (Moretto 2013a).
Group 28: West African species group.
Group 29: Sahel species group.
Group 30: Accounts for two SW African centred species.
Group 31: Subgenus, *Furconthophagus* Zunino, 1979; accounts for seven species endemic to South Africa (4) or more widely distributed (3); many others without validated names.
Group 32: See genera, *Hamonthophagus* Roggero, Dierkens, Barbero & Palestrini, 2016, or, *Morettius* Roggero, Dierkens, Barbero & Palestrini, 2016 (which is not represented in southern Africa).

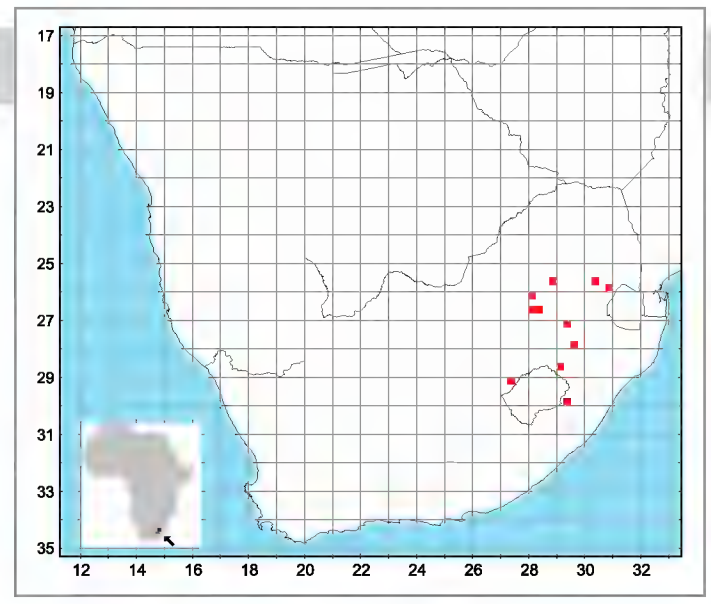
Onthophagus absyrtus

Balthasar, 1946

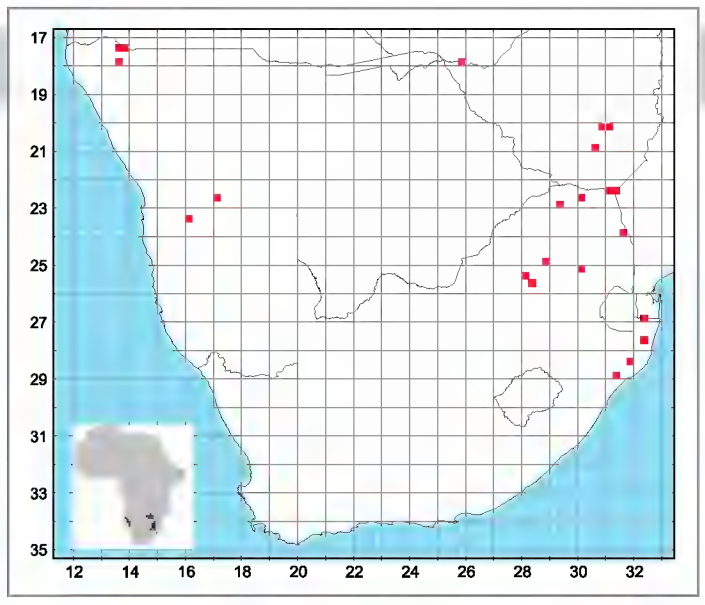
No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: 'Africa mér., Johannesburg' [South Africa: Johannesburg].
Taxonomy: Accepted species; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.
Distribution: Moist highland and montane grassland in the N Highveld, South Africa.
Locality data (mean ± SD, range): Altitude: 1 556 ± 248, 1 135–1 836 m; annual rainfall: 759 ± 139, 638–1 157 mm; annual temperature (max. + min. /2): 15.5 ± 1.8, 13.1–18.9°C (N=11).
Habitat: No quantitative assessment; limited DBRU collection records all from sandy clay loam (3) in pasture (2), fallow crop field (1).
Food types: No quantitative assessment; DBRU collection records from dung of cattle (3), human/cattle mix (1).
Temporal activity: Diel flight periodicity unknown; recorded primarily in the summer rainy season (Sept. to Jan.).
Bioregions South Africa: Primarily around the margins of Mesic Highveld Grassland (Gm) (Grassland Biome).
Assessment rationale: EOO = 65 350 km^2; AOO may be much smaller due to specialisation to very fine-grained soils; restricted AOO in moist highland grassland may also account for rarity in collections; however, quantitative data is required to support severely limited observations; currently assessed as Data Deficient (DD).
Conservation measures: Before an assessment of conservation status may be made, it is necessary to make a more precise measurement of EOO/AOO and to obtain quantitative data on ecological associations plus possible influence of habitat transformation; protected in Suikerbosrand and Telperion nature reserves, Gauteng.



Onthophagus aequepubens

d'Orbigny, 1905

No synonyms

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Nyassa' [Lake Malawi region].

Taxonomy: Accepted Group 2 species; sexually dimorphic (head), characters vary in prominence with body size.

Distribution: Apparent disjunct distribution pattern within southern African lowland savanna; possibly a collection artefact or possibly related to soil and vegetation type specialisation: South Africa, Namibia, Zimbabwe; type locality possibly Malawi.

Locality data (mean ± SD, range): Altitude: 780 ± 445, 55–1 730 m; annual rainfall: 570 ± 192, 125–988 mm; annual temperature (max. + min. /2): 20.5 ± 2.3, 17.2–24.5°C (N=25).

Habitat: In Gauteng bushveld: extreme specialisation to deep sand (142) compared to sandy clay loam (0), extreme specialisation to shaded thicket (141) compared to open woodland (1) and grassland (0); soil association not supported in uMkhuze Game Reserve: sand (0.5), sand over clay (0.3), sandy clay loam (0.5), clay (1.3) but 100% in shade (12); severely limited DBRU collection records on sand (1), clay (1) in woodland (1) and forest (2).

Food types: No quantitative assessment; DBRU collection records on dung of baboon (1), human/cattle mix (3), horse (2), cattle (2).

Temporal activity: Diurnal flight activity; in Gauteng: peak activity early in the summer rainy season (Oct. to Jan.), rare thereafter (Feb., March); also recorded during Aug. in warmer coastal region (iMfolozi Game Reserve).

Ecoregions Namibia, Zimbabwe: Southern Miombo Woodlands (AT0719), riverine vegetation of Zambezian and Mopane Woodlands (AT0725), Namibian Savanna Woodlands (AT1316).

Bioregions South Africa: Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 245 690 km² (underestimated); some support for soil specialisation; clearance of dense woody vegetation would be detrimental owing to shade specialisation; transformation in South Africa amounts to 0–58% (SVl), 2–49% (SVcb), 0–20% (SVmp); however, owing to widespread range and occurrence in both farmland and game reserves, currently assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by further quantitative data to resolve conflict in soil association data; quantitative data on food associations would also be useful; protected in Kruger National Park (South Africa), Lake Mutirikwe Game Reserve (Zimbabwe).

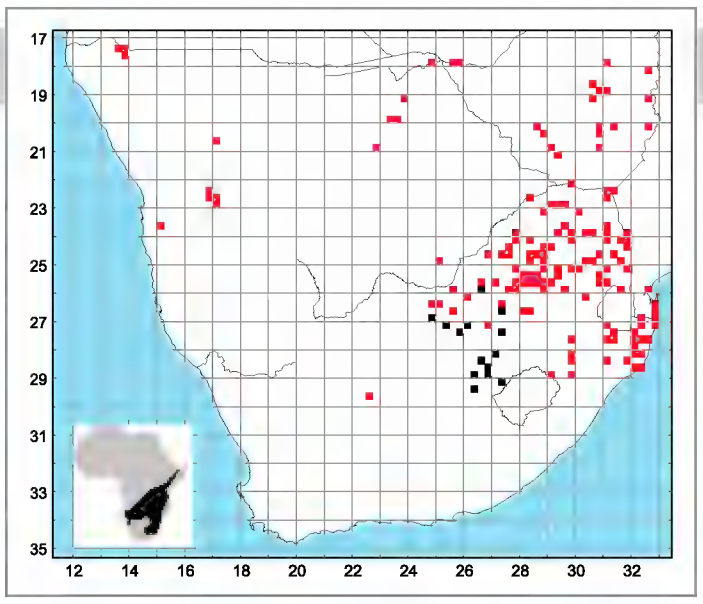
Onthophagus aeruginosus

Roth, 1851

= *Onthophagus tenuicornis* Klug, 1855
= *Onthophagus chalcostomus* Fahraeus, 1857
= *Onthophagus aeruginosus* var. *janthinus* d'Orbigny, 1902

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: 'Tigré in N. Abyssinien' [Tigray, N Ethiopia]; *O. tenuicornis*: 'Sena' [central Mozambique]; *O. chalcostomus*: 'prope fluvium Limpopo' [close to Limpopo River; southern Africa]; var. *janthinus*: 'Ouarsangueli' [N Somalia].

Taxonomy: Accepted Group 2 species; colour variation: usually iridescent green, occasionally cupreous or blueish, but melanic on South African Highveld; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.

Distribution: Mainly dry S to NE African savanna or grassland: South Africa, Namibia, Botswana, Angola, Zimbabwe, Malawi, Mozambique, Tanzania, Kenya, Ethiopia, Somalia; also reported from Rwanda, Burundi, Democratic Republic of the Congo (DRC), Eritrea; report from Guinea (Bissau) presumably an error; melanic var. (black squares), green var. (red squares) with central South African outlier in Orange River Valley.

Locality data (mean ± SD, range): Green var.: Altitude: 905 ± 530, 0–2 274 m; annual rainfall: 670 ± 175, 34–1 415 mm; annual temperature (max. + min. /2): 19.6 ± 2.4, 10.1–25.2°C (N=208). Melanic var.: Altitude: 1 406 ± 119, 1 240–1 721 m; annual rainfall: 569 ± 70, 452–703 mm; annual temperature (max. + min. /2): 16.6 ± 1.0, 14.4–18.3°C (N=14).

Habitat: Relative soil generalist with bias to woody vegetation; in Gauteng bushveld; sand (1 467), sandy clay loam (1 065), grassland (371), open woodland (1 209), shaded thickets (952); in uMkhuze Game Reserve; sand (14.8), duplex soil (sand over clay) (30.3), sandy clay loam (13.9), clay (17.3); supported by DBRU collection records: sand (20), sandy loam (18), sandy clay loam (16), clay (4) in grassland/pasture (19 – including 10 for melanic var.), shrubland (9), open woodland (14), forest/thickets (13).

Food types: At Phalaborwa: bias to omnivore dung (pig: 185) over herbivore dung (elephant: 84, cattle: 72); DBRU collection records from various dung types: cattle (45), wildebeest (1), waterbuck (1), impala (1), elephant (3), rhinoceros (3), zebra (1), horse (1), warthog (2), baboon (1), human (1), human/cattle mixture (18).

Temporal activity: Diurnal flight activity throughout the year; in Gauteng bushveld: peak flight activity late morning (10:00–12:00) with peak seasonal activity early in the summer rainy season (Oct. to Jan.) declining a little (Feb. to April) to low (May, June) and very low levels in the cool dry season (July to Sept.); at Phalaborwa: equally active in warm sunny conditions soon after heavy rainfall (178) or warm cloudy conditions soon after light rainfall (171), less active under hot dry conditions (92).

Ecoregions Namibia, Botswana, Zimbabwe, Mozambique: Namibian Savanna Woodlands (AT1316), NW Kalahari Xeric Savanna (AT1309), Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian and Mopane Woodlands (AT0725), Southern African Bushveld (AT0717),

Onthophagus aeruginosus (continued)

Southern Miombo Woodlands (AT0719), Maputaland Coastal Forest Mosaic (AT0119), margins of one other ecoregion.

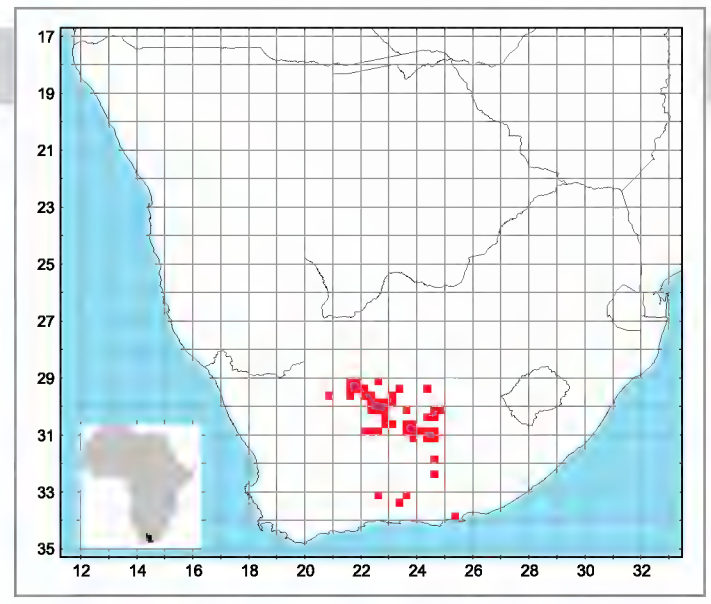
Bioregions South Africa: Central Bushveld (SVcb), Lowveld (SVl), Mopane (SVmp) (Savanna Biome); N Dry Highveld Grassland (Gh), N Mesic Highveld Grassland (Gm), N Sub-Escarpment Grassland (Gs) (Grassland Biome); N Indian Ocean Coastal Belt Biome (CB); marginal in two other bioregions; melanic var. in Dry Highveld Grassland (Gh).

Assessment rationale: EOO = 4 968 210 km^2 (underestimated gross estimate); widespread, soil and vegetation generalist found abundantly on various dung types in both farmland and reserves; assessed as Least Concern (LC).

Conservation measures: None required; protected in many reserves including Kruger National Park (South Africa).

Onthophagus albipennis

Péringuey, 1908

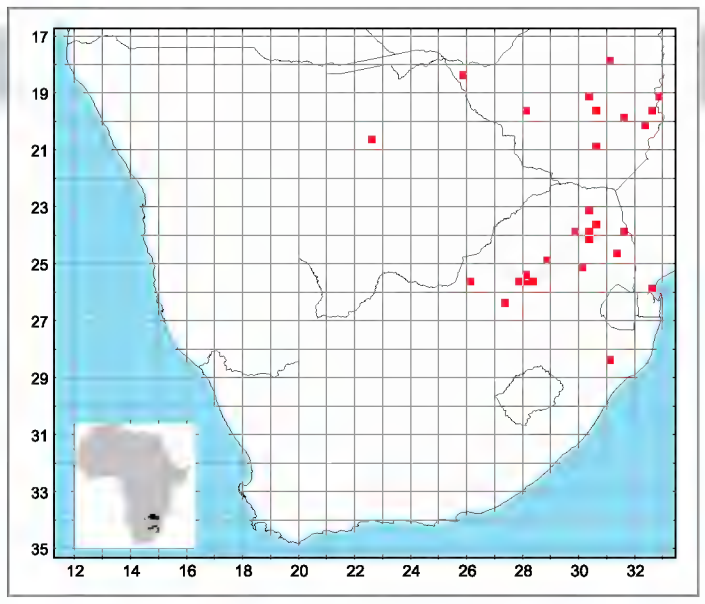


No synonyms

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Cape Colony (Uitenhage)' [Eastern Cape, South Africa].
Taxonomy: Accepted Group 11 species.
Distribution: Arid to dry areas in S late summer rainfall region and drier parts of bimodal rainfall region: Northern and Eastern Cape, South Africa; absence of records from arid terrain between coastal hinterland and Northern Cape uplands may or may not be a collecting artefact (see habitat notes below).
Locality data (mean ± SD, range): Altitude: 1 158 ± 209, 121–1 598 m; annual rainfall: 245 ± 53, 133–427 mm; annual temperature (max. + min. /2): 17.0 ± 1.7, 14.0–19.4°C (N=113).
Habitat: No adequate quantitative assessment; in Northern Cape: primarily in uplands to S of Orange River (76.7% = 66 out of 86 traps, 4.3/trap) and in Upper Karoo (92.1% = 115 out of 126 traps, 18.0/trap), few in arid lowlands of Bushmanland (4.5% = 3 out of 67 traps, 0.01/trap); also in Northern Cape: recorded on sand (15.8/trap, N=72), sandy loam (15.1, N=66), sandy clay loam (17.4, N=19); DBRU collecting records from sand (4), sandy loam (3), sandy clay loam (1) in grassland/pasture (2), scrub (4), open woodland (2).
Food types: No quantitative assessment; sampled to composite cattle/sheep baits; DBRU collection records on cattle dung (5).
Temporal activity: Diurnal flight activity during the late summer rainy season (Dec. to May).
Bioregions South Africa: Bushmanland (NKb), Upper Karoo (NKu) (Nama Karoo Biome), also margins of both Rainshadow Valley Karoo (SKv) (Succulent Karoo Biome) and Albany Thicket Biome (AT).
Assessment rationale: EOO = 126 235 km^2; widespread soil generalist with high frequency and high abundance in upland Karoo; not recorded in more arid lower areas; N part of range little transformed and used primarily for grazing domestic livestock that drop dung to which it is readily attracted; assessed as Least Concern (LC).
Conservation measures: Assessment of conservation status would be improved by a survey to determine the limits of the EOO, particularly if the species is also characteristic of the arid Lower Karoo; formal assessment of ecological associations would also assist; not currently recorded from any reserve.



Onthophagus albipodex

d'Orbigny, 1902

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Lake Ngami' [Botswana].

Taxonomy: Accepted Group 24 species, but research required on relationships to species of similar appearance described from further N and further SW; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.

Distribution: Moist savanna regions of SE Africa; apparent disjunction across the hot, dry Limpopo Valley may be real or a collection artefact; type locality is an outlier at W edge of range: South Africa, Zimbabwe, Mozambique, Botswana; also cited from Malawi; citation from Angola requires validation.

Locality data (mean ± SD, range): Altitude: 988 ± 379, 11–1 510 m; annual rainfall: 686 ± 123, 414–1 100 mm; annual temperature (max. + min. /2): 19.6 ± 2.0, 16.7–24.4°C (N=37).

Habitat: In Gauteng bushveld: bias to deep sand (15) compared to sandy clay loam (2), bias to grassland (14) compared to open woodland (3) or shaded thicket (0); only partly supported by limited DBRU collection records: sandy loam (3), sandy clay loam (4) in grassland/pasture (6), shrubland (2).

Food types: No quantitative assessment; DBRU collection records: dung of cattle (9), human (1), human/cattle mix (1).

Temporal activity: Diurnal flight activity in the summer rainy season (Oct. to Feb.); in Gauteng bushveld: only active in early rainy season (Oct. to Dec.).

Ecoregions Botswana, Zimbabwe: Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian Baikiaea Woodlands (AT0726), Southern Miombo Woodlands (AT0719), margins of one other ecoregion.

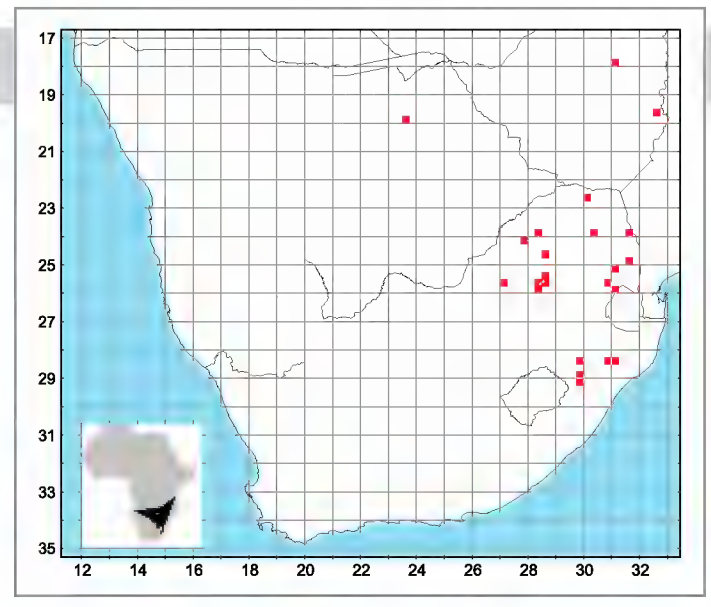
Bioregions South Africa: Central Bushveld (SVcb), Lowveld (SVl), Mopane (SVmp) (Savanna Biome); N margins Dry Highveld Grassland (Gh) (Grassland Biome).

Assessment rationale: EOO = 324 950 km² (probably underestimated); widespread, but recorded in relatively low population density throughout its range; conflicting soil association data negate any conclusions on specialisation or generalisation; may not be unduly influenced by clearance of woodland owing to apparent association with open vegetation; not common, but also not rare; currently assessed as Least Concern (LC).

Conservation measures: Further quantitative data on ecological associations is required to improve assessment of conservation status, particularly to determine if AOO is influenced by soil type; protected in Kruger National Park and Tswaing Nature Reserve (South Africa).

Onthophagus apiciosus

d'Orbigny, 1902



No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Afrique orientale allemande' [Tanzania].

Taxonomy: Accepted Group 19 species, but distribution requires validation as often confused with other close relatives; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.

Distribution: Moist savanna from southern to East Africa: South Africa, Angola, Botswana, Zimbabwe, Mozambique, Malawi, Zambia, Tanzania; also reported from Democratic Republic of the Congo (DRC), Kenya.

Locality data (mean ± SD, range): Altitude: 1 038 ± 360, 266–1 698 m; annual rainfall: 709 ± 151, 416–1 130 mm; annual temperature (max. + min. /2): 19.2 ± 1.9, 16.7–23.7°C (N=33).

Habitat: No quantitative assessment; limited DBRU collection records from sand (1), sandy loam (1), clay (1) in pasture (1), open woodland (1), forest (1), even an orchard (1).

Food types: No quantitative assessment; limited DBRU collection records from human/cattle dung mixture (2); but see Assessment rationale.

Temporal activity: Flight activity in darkness during the summer rainy season (Oct. to Apr.); attracted to light.

Ecoregions Botswana, Zimbabwe: Zambezian and Mopane Woodlands (AT0725), Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Central Bushveld (SVcb), Lowveld (SVl), Mopane (SVmp) (Savanna Biome); N Sub-Escarpment Grassland (Gs) (Grassland Biome).

Assessment rationale: EOO = 2 057 540 km^2; AOO unclear; ecologically poorly known owing to lack of quantitative data, but Group 19 is thought to be characterised primarily by carrion associations; easily confused with putative close relatives, but probably widespread possibly with generalist habitat associations; therefore, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status needs to be improved by quantitative ecological data to confirm generalist habitat associations with omnivore dung and/or carrion specialisation; protected in Kruger National Park (South Africa).

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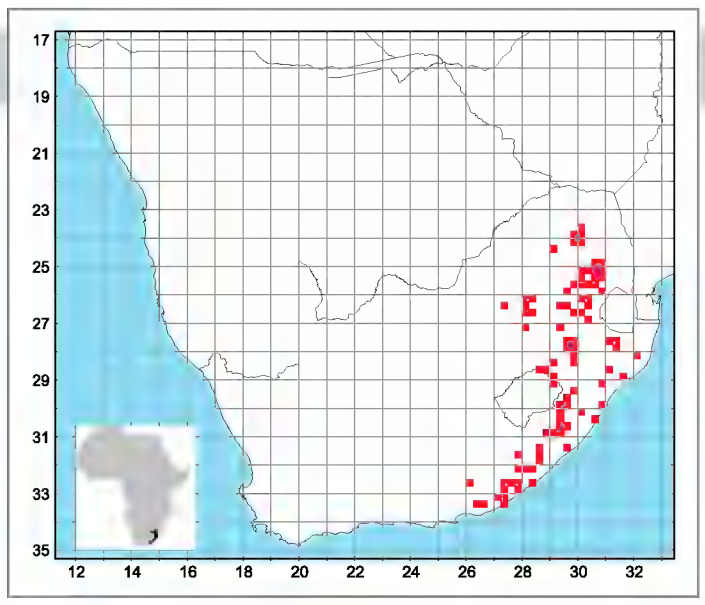


Onthophagus asperulus

d'Orbigny, 1905

No synonyms

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'Transvaal: Boksburg.....Johannesburg....Natal: Malvern' [South Africa: Gauteng, KwaZulu-Natal].

Taxonomy: Accepted Group 23 species, but status needs to be validated or revised after comparison with *O. impictus* Fahraeus, 1857, and *O. scabrosus* Péringuey, 1901 (both from type localities in KwaZulu-Natal) that are currently synonymised with *O. hyaena* (Fabricius, 1801: S Eastern Cape and Free State range), but probably in error; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.

Distribution: Coast and uplands along SE seaboard (E Eastern Cape, KwaZulu-Natal), N Highveld (Gauteng, Mpumalanga, Limpopo); South Africa.

Locality data (mean ± SD, range): Altitude: 1 241 ± 533, 46–2 392 m; annual rainfall: 779 ± 117, 517–1 136 mm; annual temperature (max. + min. /2): 16.0 ± 1.9, 9.9–21.4°C (N=139).

Habitat: No adequate quantitative assessment; in Suikerbosrand Nature Reserve: montane grassland 1 888–1 930 m (3.9 per sample), Highveld Grassland 1 631–1 685 m (8.7), open woodland 1 637–1 689 m (1.4); at 1 496–1 541 m in Abe Bailey Nature Reserve: grassland (16.3), open woodland (2.9); at Carolina in Jan.: natural *Themeda* grassland (28.5), rehabilitating crop field (25.2), improved Kikuyu pasture (109.0); DBRU collection records: sand (2), sandy loam (31), sandy clay loam (44), clay (5) in grassland/pasture (75), shrubland (1), open woodland (2), fallow crop field (3).

Food types: No quantitative assessment; DBRU collection records on dung of cattle (84), horse (1), human/cattle mix (1).

Temporal activity: Diurnal flight activity, primarily during the summer rainy season (Aug. to May).

Bioregions South Africa: N Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs) (Grassland Biome); Indian Ocean Coastal Belt Biome (CB); E Albany Thicket Biome (AT).

Assessment rationale: EOO = 170 285 km^2; widespread in farmland from the warmer, moister N and E Highveld to the SE coast where it is readily attracted to the dung of farm livestock and is not negatively influenced by pasture improvement; assessed as Least Concern (LC).

Conservation measures: Attention needs to be paid to taxonomic issues with nomenclature; assessment of conservation status would be improved by quantitative data on ecological associations; protected in various nature and game reserves including Suikerbosrand, Abe Bailey, Ithala, Vernon Crookes.

Onthophagus axillaris

Boheman, 1860

Onthophagus criniger

d'Orbigny, 1904

= *Onthophagus crinitus* d'Orbigny, 1902

Global: DD

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. axillaris* Boheman: 'in regione fluvii Svakop' [Swakop River region, W Central Namibia]; *O. criniger*, *nom. nov.* for *O. crinitus* (pre-occupied name): 'Lac Ngami' [Lake Ngami, N Botswana].

Taxonomy: Both cited as accepted Group 16 species, but very closely related; current status of Péringuey's (1908) synonymy of *O. criniger* with *O. axillaris* unclear; to validate species-level separation, types of both need to be re-examined, perhaps together with NE African (*O. pilicollis* d'Orbigny, 1902) and W Central African relatives (*O. hirsutus* d'Orbigny, 1902), minor sexual dimorphism (head).

Distribution: *O. axillaris*: dry to moist savanna: NW Namibia (red squares) and SW Angola; *O. criniger*: dry to moist savanna: N Botswana (black square) and edge of Zambezi Valley in Zimbabwe and Malawi.

Locality data (mean ± SD, range): Combined: altitude: 1 249 ± 461, 1–1 998 m; annual rainfall: 415 ± 276, 9–1 256 mm; annual temperature (max. + min. /2): 18.8 ± 1.9, 15.8–22.4°C (N=20+3).

Habitat: No quantitative assessment; DBRU collection records on sand (2), sandy loam (4) in grassland (2), open woodland (4).

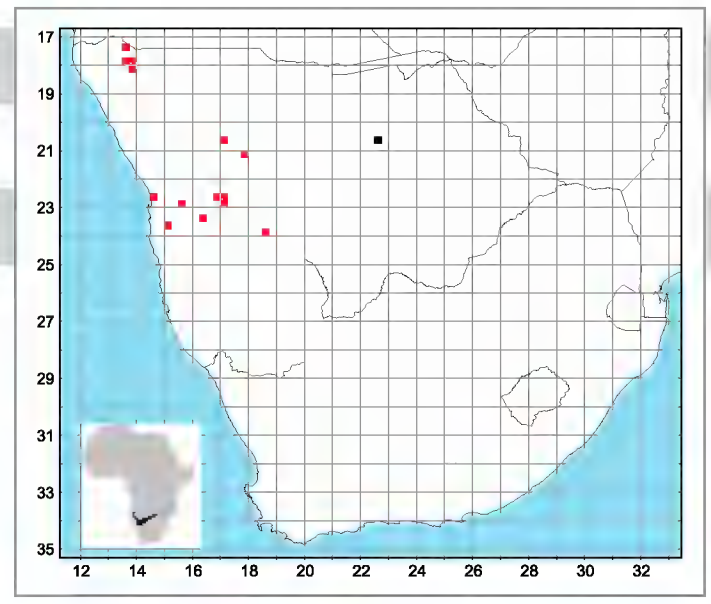
Food types: No quantitative assessment; DBRU collection records on dung of cattle (4), elephant (2), zebra (1).

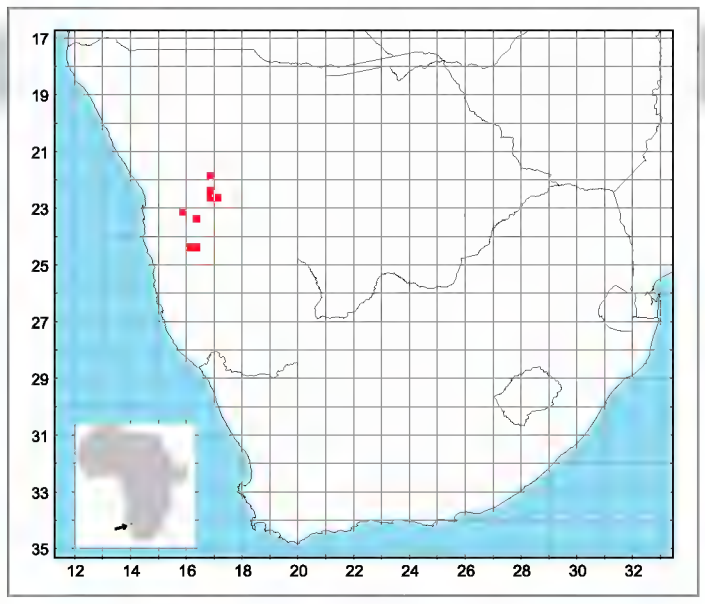
Temporal activity: Diurnal flight activity, primarily during mid- and late summer rainy seasons (Oct. to June).

Ecoregions Namibia, Botswana: *O. axillaris*: Namib Desert (AT1315), Namibian Savanna Woodlands (AT1316), NW Kalahari Xeric Savanna (AT1309), Angolan Mopane Woodlands (AT0702); *O. criniger*: Kalahari Acacia-Baikiaea Woodlands (AT0709).

Assessment rationale: Combined EOO = 393 675 km²; despite close similarities in appearance, taxonomic uncertainty and differences in vegetation associations between the two 'species' renders it difficult to assess conservation status; therefore, assessed as Data Deficient (DD), but populations identified as *O. axillaris* probably deserve an assessment as Least Concern (LC) as most records are from areas that are little transformed.

Conservation measures: To generate an assessment of conservation status, taxonomic issues need to be resolved; quantitative data on ecological associations would also improve any assessment; populations identified as *O. axillaris* protected in Bicuar National Park, Angola; Namibian populations primarily recorded from farm rangeland.





Onthophagus bayeri

Balthasar, 1942

No synonyms

Global: DD
Endemic: Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Süd-West Afrika, Okahandja' [Okahandja, Namibia].
Taxonomy: Accepted Group 18 species; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.
Distribution: Arid to dry uplands and highlands: central Namibia.
Locality data (mean ± SD, range): Altitude: 1 520 ± 252, 1 144–1 815 m; annual rainfall: 240 ± 92, 136–353 mm; annual temperature (max. + min. /2): 17.6 ± 1.5, 15.8–19.8°C (N=8).
Habitat: Not known.
Food types: No quantitative assessment; reference material recorded from baits of human dung and meat; a few from banana.
Temporal activity: Diel flight activity unknown; recorded primarily in the summer rainy season (Oct. to Mar.).
Ecoregions Namibia: NW Kalahari Xeric Savanna (AT1309), S Central Namibian Savanna Woodlands (AT1316).
Assessment rationale: EOO = 10 885 km²; known from only eight localities across a range of < 20 000 km²; limited records may be related to food specialisation as close relatives in Group 18 are carrion specialists; although probably not threatened at present, supporting quantitative survey data are required; currently assessed as Data Deficient (DD).
Conservation measures: To assess conservation status, quantitative data are required to determine the full EOO, AOO and ecological associations; W edge of range coincides with E edge of Namib-Naukluft Park, but most records lay outside of protected areas.

♂

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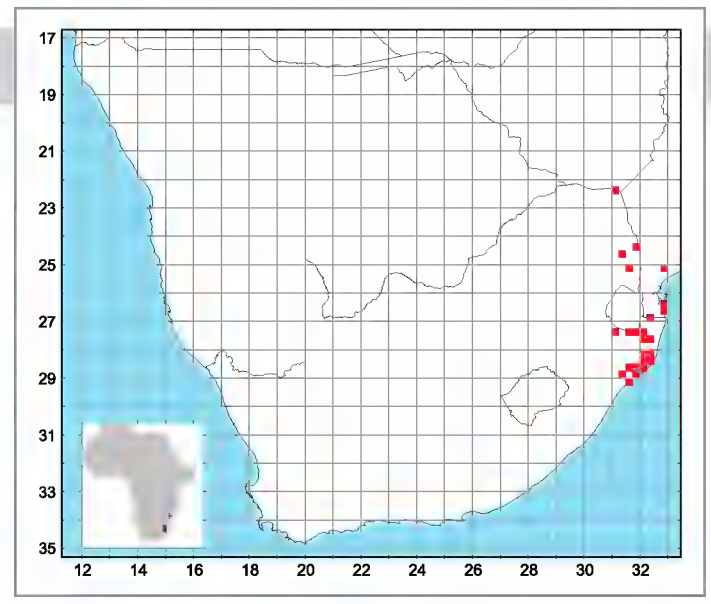
Onthophagus beiranus

Péringuey, 1908



No synonyms

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'Mozambique (Beira; Lucitania)' [Mozambique: Beira and Búzi].

Taxonomy: Accepted Group 7 species belonging to the new subgenus, *Bicornonthophagus* Tagliaferri & Moretto, 2012; needs to be compared with *O. auriculatus* Klug, 1855 (type locality: Tete, Mozambique) and *O. insulsus* Péringuey, 1901 (type locality: Eshowe, KwaZulu-Natal, South Africa); sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.

Distribution: Disjunct and scattered occurrence on floodplains and in savanna woodlands and thicket of the Mozambique Coastal Plain owing to soil type specialisation: South Africa, Mozambique.

Locality data (mean ± SD, range): Altitude: 154 ± 194, 0–1 005 m; annual rainfall: 887 ± 225, 396–1 275 mm; annual temperature (max. + min. /2): 22.3 ± 1.7, 17.8–25.2°C (N=47).

Habitat: In uMkhuze Game Reserve: strong bias to clay (46.7) compared to sandy clay loam (2.3), sand over clay (7.3), and deep sand (0.1); supported by DBRU collection records: clay (11), sandy clay loam (12), sand (3) on grassland/pasture (11), open woodland/dense woodland (12), shaded thicket (3).

Food types: No quantitative assessment; DBRU collection records from dung of cattle (13), buffalo (2), wildebeest (2), elephant (4), zebra (2), waterbuck (2).

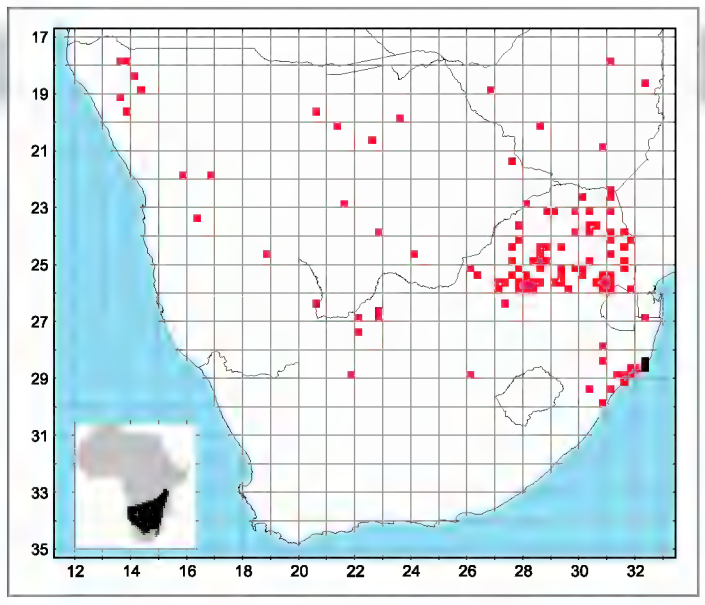
Temporal activity: Flight activity in darkness primarily during the rainy season (Oct. to Apr.), but with some dry season activity across the warm lowland range.

Ecoregions Mozambique: Maputaland Coastal Forest Mosaic (AT0119), also Zambezian Coastal Flooded Savanna (AT0906), Southern Zanzibar-Inhambane Coastal Forest Mosaic (AT0128) (not shown on map).

Bioregions South Africa: Lowveld (SVl) (Savanna Biome); N Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 98 720 km^2; disjunct EOO based on known records; AOO would be smaller coinciding with finer-grained soils separated by large expanses of sandy soils; however, observed to be abundant in cattle pads on Pungwe Flood Plain near Muda, Mozambique; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by further survey data to determine if known disjunct distribution pattern is a collecting artefact; quantitative data on vegetation and dung type associations would also be useful; protected in uMkhuze Game Reserve.



Onthophagus bicavifrons

d'Orbigny, 1902

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'Afrique orientale allemande: Ouzambara....; lac Ngami.., Zoulouland..; Natal: Durban' [Usambara Mts, Tanzania; Lake Ngami, Botswana; Zululand and Durban, South Africa].

Taxonomy: Accepted Group 18 species, but species cited here as *O. bicavifrons* requires validation by comparison with type(s); sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size; SE coastal variety more densely punctate, but aedeagus identical (black squares).

Distribution: Widespread in moist savanna from S to E Africa: South Africa, Namibia, Botswana, Zimbabwe, Angola, Tanzania; also reported from Mozambique, Malawi, Democratic Republic of the Congo (DRC), Kenya.

Locality data (mean ± SD, range): Altitude: 928 ± 452, 0–1 733 m; annual rainfall: 633 ± 206, 171–1 157 mm; annual temperature (max. + min. /2): 19.6 ± 2.1, 14.0–25.2°C (N=149).

Habitat: No quantitative assessment; available DBRU records too limited to determine trends: sand (3), sandy clay loam (1) in grassland/pasture (3), shrubland (1), forest (1).

Food types: In Botswana: attracted only to carrion (chicken livers: 7), not to dung (pig, elephant, cattle, sheep); limited DBRU collection records on dead millipede (4), impala gut contents (1); also dung of horse (1), cattle (1).

Temporal activity: Flight activity in darkness during the summer rainy season (Oct. to Apr.); attracted to light.

Ecoregions Namibia, Botswana, Zimbabwe: Namibian Savanna Woodlands (AT1316), Kalahari Xeric Savanna (AT1309), Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian and Mopane Woodlands (AT0725), marginal in two other ecoregions.

Bioregions South Africa: Primarily, Indian Ocean Coastal Belt Biome (CB), Central Bushveld (SVcb), Lowveld (SVl), Mopane (SVmp), also Eastern Kalahari Bushveld (SVk) (Savanna Biome) with scattered records in five other bioregions.

Assessment rationale: EOO = 4 290 470 km^2; extremely widespread, assuming records to the N represent a single species; trophic records suggest a carrion specialist whereas the wide scatter of records suggest habitat generalisation, but support is severely limited; unlikely to face any threats over most of range; assessed as Least Concern (LC) on basis of available data.

Conservation measures: Assessment of conservation status would be improved by quantitative data on habitat associations and stronger support for carrion associations; protected in the Kruger National Park (South Africa).

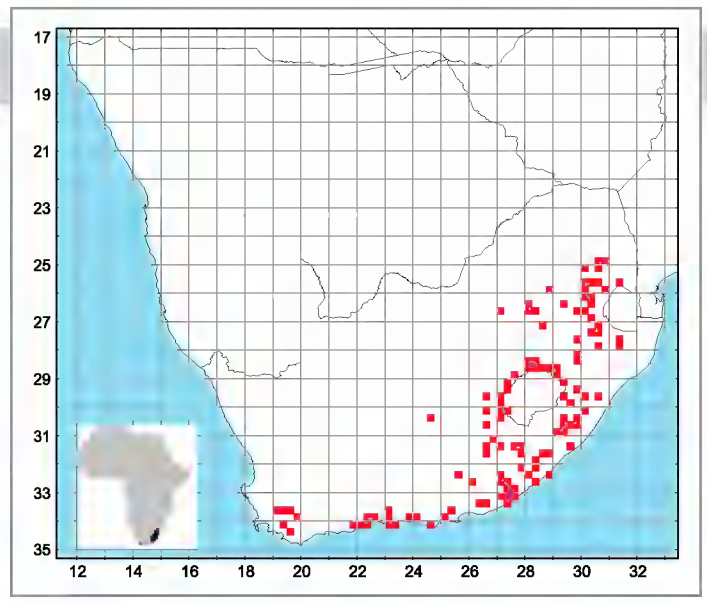
Onthophagus binodis

(Thunberg, 1818)

= *Onthophagus columella* Fahraeus, 1857

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: As *Copris binodis*: 'majorem horum partem in capite bonae spei collegi' [amongst material mostly collected in the Cape of Good Hope, South Africa]; *O. columella*: 'Boschiesmans Rand' [Bushmans Ridge = uncertain location].

Taxonomy: Accepted Group 4 species; sexually dimorphic (prothoracic disc), character varies in prominence with body size.

Distribution: Cool, moist, E Highveld descending to coastal regions of the Eastern and Western Cape in the S: South Africa, Lesotho; introduced into Australia.

Locality data (mean ± SD, range): Altitude: 1 092 ± 621, 0–2 286 m; annual rainfall: 669 ± 167, 293–1 101 mm; annual temperature (max. + min. /2): 15.9 ± 1.7, 10.6–22.5°C (N=160).

Habitat: No adequate quantitative assessment; at Carolina: little influenced by habitat disturbance, natural *Themeda* grassland (337), fallow crop fields (119), improved Kikuyu pasture (276); at Boschberg: much more abundant in cool Highveld Grassland at 1 676–1 687 m (2 294) than in warmer lower-altitude grassland at 1 264–1 303 m (348); DBRU collection records suggest bias to finer-grained soils in grassland: sand (9), sandy loam (28), sandy clay loam (45) in grassland/pasture (61), open shrub/woodland (4), also fallow crop fields (5).

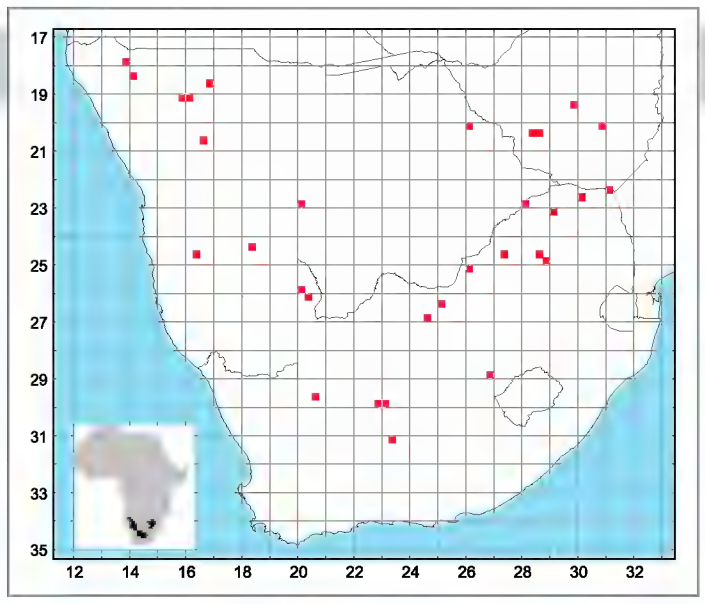
Food types: No quantitative assessment; DBRU collection records primarily from cattle dung (104), horse (1).

Temporal activity: Diurnal flight activity in spring, summer and autumn (Sept. to May) reflecting range in winter, bimodal and summer rainfall regions of South Africa.

Bioregions South Africa: Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs) (Grassland Biome); S Indian Ocean Coastal Belt Biome (CB); mostly transformed grassland habitats in moister parts of Albany Thicket Biome (AT) plus Eastern Fynbos-Renosterveld (FO 6), East Coast Renosterveld (FO 8), Southwest Fynbos (FO 2) bioregions (Fynbos Biome).

Assessment rationale: EOO = 274 485 km^2; widespread and abundant in both natural and transformed farm grasslands; occurrence primarily in transformed pasture habitats in Fynbos, Renosterveld and Albany Thicket may indicate range expansion in response to clearance of natural shrubland; assessed as Least Concern (LC).

Conservation measures: Not currently threatened, but assessment of conservation status would be improved by further quantitative data on ecological associations, including tests of grassland versus shrubland association in the S; protected in Suikerbosrand Nature Reserve, Golden Gate National Park and lower-altitude parts of Ukhahlamba Drakensberg Park (World Heritage Site).



Onthophagus bovinus

Péringuey, 1892

= *Onthophagus lobigena* d'Orbigny, 1902

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. bovinus*: Not stated, but possibly Ovamboland, Namibia; *O. lobigena*: 'Natal' [KwaZulu-Natal, South Africa].

Taxonomy: Accepted Group 7 species; synonymy of *O. lobigena* should be re-examined as type locality of 'Natal' lies outside known range of *O. bovinus*; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.

Distribution: Arid Karoo to dry savanna along a wide band of terrain encompassing the E, S and W borders of the deep Kalahari sands: Namibia, South Africa, Botswana, Zimbabwe.

Locality data (mean ± SD, range): Altitude: 1 093 ± 282, 243–1 530 m; annual rainfall: 416 ± 162, 124–674 mm; annual temperature (max. + min. /2): 19.8 ± 2.2, 15.5–24.3°C (N=32).

Habitat: No quantitative data; limited DBRU collection records on sand (4), sandy clay loam (3) in grassland (3), open shrub/woodland (4).

Food types: No quantitative data; limited DBRU collection records on dung of cattle (3), wildebeest (1), elephant (1), human/cattle mix (1).

Temporal activity: Flight activity in darkness during the summer rainy season (Nov. to May); attracted to light.

Ecoregions Namibia, Botswana, Zimbabwe: Namibian Savanna Woodlands (AT1316), Kalahari Xeric Savanna (AT1309), Angolan Mopane Woodlands (AT0702), Kalahari Acacia-Baikiaea Woodlands (AT0709), Southern African Bushveld (AT0717), Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Bushmanland (NKb), Upper Karoo (NKu) (Nama Karoo Biome); Kalahari Duneveld (SVkd), Eastern Kalahari Bushveld (SVk), Central Bushveld (SVcb), Mopane (SVmp) (Savanna Biome); Dry Highveld Grassland (Gh) (Grassland Biome).

Assessment rationale: EOO = 642 681 km^2; recorded across a wide area on a range of dung types in relatively open vegetation on both coarse and fine-grained soil types; arid part of range little transformed; currently assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be much improved by taxonomic re-examination and quantitative data on ecological associations; protected in Etosha National Park (Namibia), Kgalagadi Transfrontier Park (South Africa/Botswana).

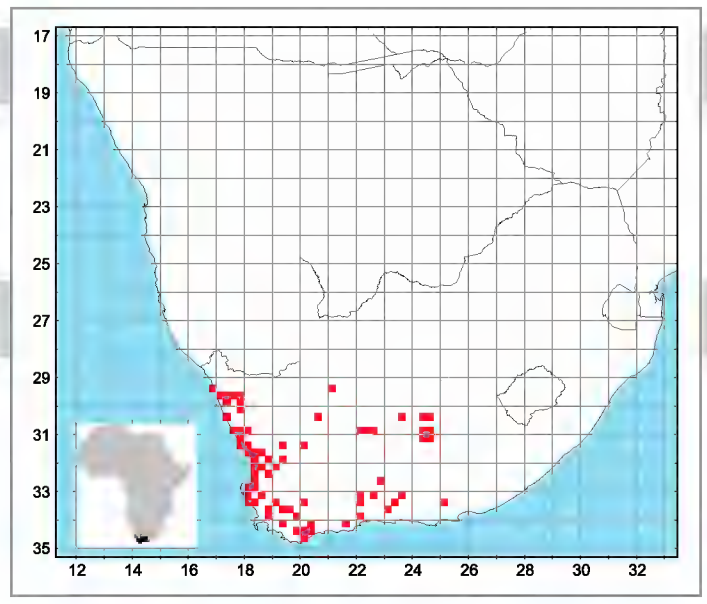
Onthophagus cameloides

d'Orbigny, 1900

= *Onthophagus urus* Harold, 1867c

Onthophagus quadricallosus

d'Orbigny, 1902



Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. cameloides*: *nom nov.* for *O. urus* [pre-occupied name] 'Cap der guten Hoffnung'; *O. quadricallosus*: 'Cap de Bonne-Espérance' [both Cape of Good Hope, South Africa].

Taxonomy: Accepted Group 30 species, but needs to be re-examined as a possible senior name for *O. quadricallosus*, which d'Orbigny described from a single larger specimen (8.5 mm) that is close to *O. cameloides* described from smaller specimens (4.00–5.25 mm); significance of climatic differences in seasonal activity also requires investigation; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.

Distribution: Dry to arid areas in the winter, bimodal and late summer rainfall regions of South Africa; absence of records from central S Nama Karoo possibly a collection artefact; claimed records from Java undoubtedly an error.

Locality data (mean ± SD, range): Altitude: 506 ± 495, 1–1598 m; annual rainfall: 237 ± 98, 63–445 mm; annual temperature (max. + min. /2): 16.8 ± 1.3, 14.0–20.0°C (N=97).

Habitat: No adequate quantitative assessment; in Western Cape: absent from cool Cape Peninsula, but on W coast near Darling Hills, more abundant in pastures (233, 123, 241) than in natural shrubland (sand: 31, sandy loam: 34), rare on coastal deep sands (9, 1, 4); DBRU collection records on sand (22), sandy loam (10), sandy clay loam (8), clay (1) in grassland/pasture (13), scrub (13), open shrub/woodland (2); also fallow crop fields (9).

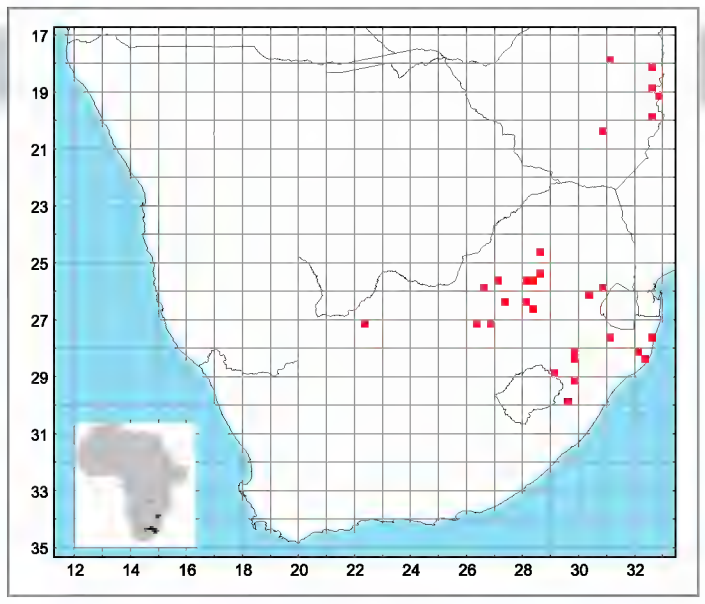
Food types: No quantitative assessment; DBRU collection records from dung of buffalo (1), cattle (40), sheep (1), horse (6), donkey (1).

Temporal activity: Diurnal flight activity; seasonal activity varies with climate; in W Coast winter rainfall region: population shows spring to early summer activity (July to Dec.); in spring: young, gravid, sclerotised adults are dominant, but population then ages; in early dry summer: callow, teneral adults with no follicular development are dominant; in Northern Cape late summer rainfall region: also recorded Mar. to May.

Bioregions South Africa: Various drier Fynbos and Renosterveld bioregions (Fynbos Biome); various bioregions of the Succulent Karoo Biome; Upper Karoo (NKu), Bushmanland (NKb) (Nama Karoo Biome).

Assessment rationale: EOO = 241 800 km^2 (inludes central S Nama Karoo); widespread association with open vegetation and tolerance of habitat transformation on various soils types together with ready attraction to dung of farm livestock suggest limited threats, particularly as transformation is limited in the N and NE of the range used primarily for livestock grazing; assessed as Least Concern (LC).

Conservation measures: None recommended although assessment of conservation status would be improved by quantitative ecological data and taxonomic revision; protected in Bontebok, West Coast and Namaqua national parks.



Onthophagus cinctipennis

Quedenfeldt, 1884

= *Onthophagus patricius* Péringuey, 1901

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. cinctipennis*: 'Malange' [Angola]; *O. patricius*: 'Natal (Estcourt)' [KwaZulu-Natal, South Africa].

Taxonomy: Accepted Group 2 species; minor sexual dimorphism (head).

Distribution: Disjunct pattern on moist SE coastline and moist SE and south central African uplands/highlands: N South Africa, E Zimbabwe, Central Mozambique, W Angola, S Democratic Republic of the Congo (DRC).

Locality data (mean ± SD, range): Altitude: 1 240 ± 439, 7–2 274 m; annual rainfall: 761 ± 210, 310–1 659 mm; annual temperature (max. + min. /2): 17.6 ± 2.1, 10.6–22.2°C (N=35).

Habitat: In Gauteng bushveld: extreme bias to deep sand (211) compared to sandy clay loam (0), in grassland (140), open woodland (53), shaded thickets (18); limited DBRU collection records support open vegetation association, grassland/pasture (5), shrubland (1), but not soil association, sand (1), sandy clay loam (5).

Food types: No quantitative assessment; limited DBRU collection records all on cattle dung (5).

Temporal activity: Diurnal flight activity, primarily during the summer rainy season, also early dry season (Oct. to June); in Gauteng bushveld: activity commencing in Oct., peaking in Dec., continuing in late rainy season (Jan. to Apr.), tailing off into the dry season; in Gauteng bushveld: active in the cooler early morning in mid-summer (08:00–10:00, Nov. to Feb.) moving to a midday flight activity window in cooler late summer (10:00–14:00, March).

Ecoregions Zimbabwe: Eastern Zimbabwean Forest Grassland Mosaic (AT1006), Southern Miombo Woodlands (AT0719).

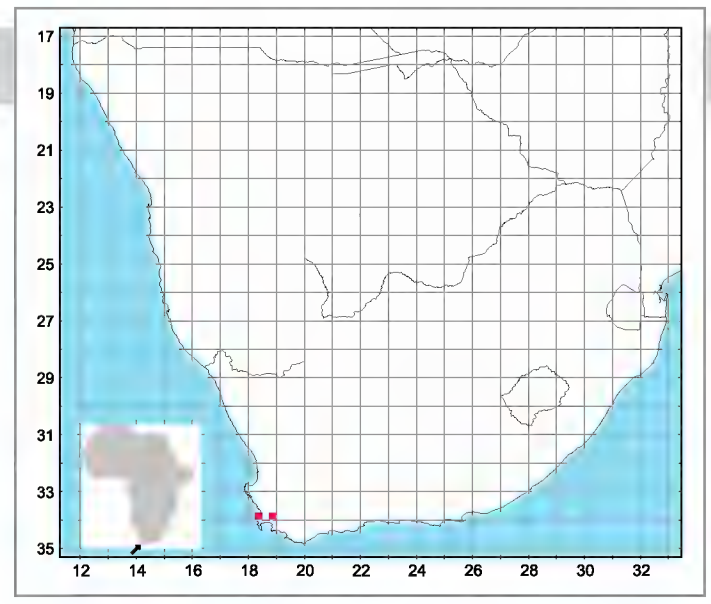
Bioregions South Africa: Primarily straddling edges of bioregions at N and NE edge of Highveld: Central Bushveld (SVcb) (Savanna Biome); Dry Highland Grassland (Gh), Mesic Highland Grassland (Gm), Sub-Escarpment Grassland (Gs) (Grassland Biome); also Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 217 320 km^2 (underestimated); possible restriction of AOO by soil specialisation requires further investigation owing to conflicting results; known highland occurrence in South Africa coincides with vegetation units subject to habitat transformation: 25–63% (Gh), 10–50% (Gs); however, widespread in open vegetation types across several moist highland blocks in southern Africa; therefore, currently assessed as Least Concern (LC)

Conservation measures: Assessment of conservation status would be improved by further quantitative data on soil and dung type association as well as possible effects of habitat transformation; limited protection in nature reserves, including Suikerbosrand (South Africa).

Onthophagus cineraceus

d'Orbigny, 1902



No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Colonie du Cap.... : Cape Town' [Western Cape, South Africa].

Taxonomy: Currently an accepted Group 9 species, but type needs to be compared with that of *O. hyaena* (Fabricius, 1801); *O. cineraceus* could possibly be a junior synonym; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.

Distribution: Currently known only from SW Western Cape in vicinity of Cape Town, South Africa, possibly in mountainous terrain; citations from KwaZulu-Natal in South Africa, Zimbabwe and Mozambique are errors.

Locality data (mean ± SD, range): Altitude: 571 ± 144, 469–673 m; annual rainfall: 473 ± 11, 465–480 mm; annual temperature (max. + min. /2): 14.4 ± 0.2, 14.3–14.6°C (N=2).

Habitat: No quantitative assessment; unknown.

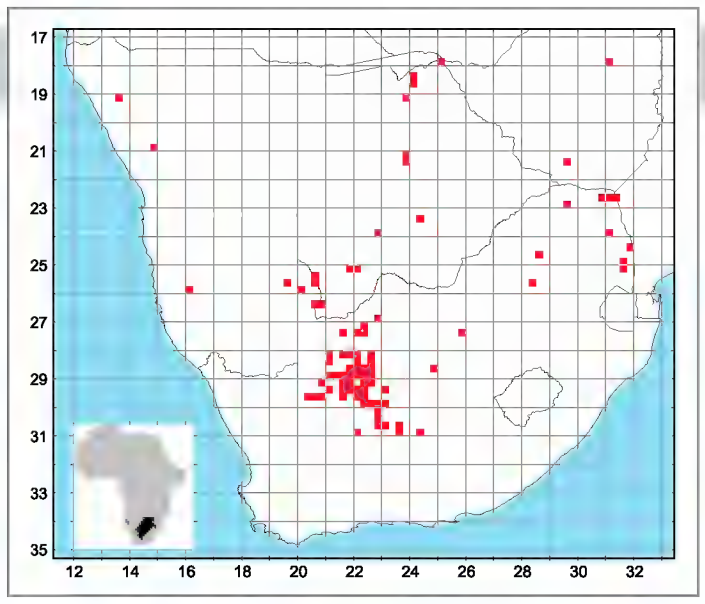
Food types: No quantitative assessment; one individual on jackal dung.

Temporal activity: Not known, but probably diurnal flight activity; recorded in the dry season of the winter rainfall region (Dec., Jan.).

Bioregions South Africa: Locality records inaccurate; possibly vegetation units comprising Peninsula Sandstone Fynbos (FFs 9) and Kogelberg Sandstone Fynbos (FFs 11) (Fynbos Biome) containing patches of Southern Afrotemperate Forest (FOz 1).

Assessment rationale: EOO = 180 km^2 (gross estimate); currently known from two localities, one old and inexact (Cape Town), the other more recent along a mountain hiking trail that passes through fynbos and segments of old forest (near Stellenbosch); considering the absence of ecological data, must be assessed as Data Deficient (DD); considering the rarity in collections and apparent small range in a highly transformed region, may deserve an IUCN threat category if surveys of the Western and Eastern Cape fail to locate the species elsewhere.

Conservation measures: Assessment of conservation status will only be possible once the EOO, AOO and ecological associations have been established; to this end, a quantitative survey of mountain fynbos and forest patches is required during early summer, commencing in the vicinity of Cape Town; protected in Jonkershoek Nature Reserve.



Onthophagus convexus

d'Orbigny, 1908

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Rhodésia: Salisbury' [Harare, Zimbabwe].

Taxonomy: Accepted Group 22 species described from a single individual; at SW edge of range, Karoo individuals shiny, but otherwise similar to NE populations; however, W populations should be compared with *Onthophagus aspericeps* d'Orbigny, 1908, described from a single Group 22 individual recorded at 'Okahandya' [Okahandja, Namibia]; description on previous page (148) to that of *O. convexus* (149); minor sexual dimorphism (head).

Distribution: Centred on sandy soils across most of southern Africa: Namibia, Botswana, Zimbabwe, South Africa.

Locality data (mean ± SD, range): Altitude: 1 015 ± 207, 278–1 410 m; annual rainfall: 279 ± 133, 88–835 mm; annual temperature (max. + min. /2): 19.3 ± 1.6, 14.7–23.7°C (N=183).

Habitat: In Gauteng bushveld: extreme association with deep sand (195) compared to sandy clay loam (0) with a bias to grassland (148) compared to open woodland (47) or shaded thickets (0) (cited as *Onthophagus* sp. nr *pullus* (a)); limited DBRU collection records on sand (4), sandy loam (2) in grassland (2), open shrub/woodland (4).

Food types: In Botswana: abundant on all dung types with a bias to omnivore dung (pig: 5 912, elephant: 2 877, cattle: 1 751, sheep: 1 931), relatively uncommon on carrion (30) (cited as *Onthophagus* sp. nr *pullus* (a)); limited DBRU collection records on dung of cattle (2), elephant (1), donkey (1), human/cattle mix (1).

Temporal activity: Diurnal flight activity during the summer rainy season (Oct. to Mar.); on Gauteng bushveld: primarily active early to mid-summer (Oct. to Jan.) becoming rare late summer (Feb., Mar.).

Ecoregions Namibia, Botswana, Zimbabwe: Kalahari Xeric savanna (AT1309), Namibian Savanna Woodlands (AT1316), Angolan Mopane Woodlands (AT0702), Kalahari Acacia-Baikiaea Woodlands (AT0809), Zambezian and Mopane Woodlands (AT0725), Southern African Bushveld (AT0717), Southern Miombo Woodlands (AT0719).

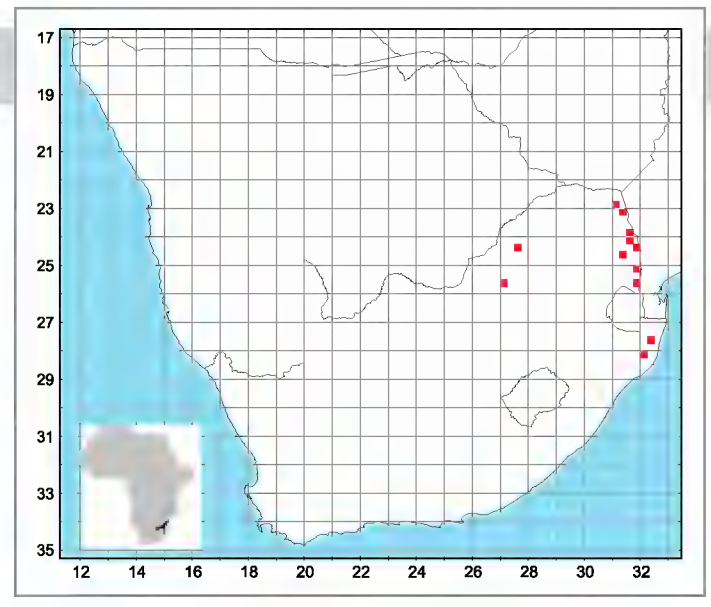
Bioregions South Africa: Sandy soils in Kalahari Duneveld (SVkd), Eastern Kalahari Bushveld (SVk), Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome); Bushmanland (NKb), NW Upper Karoo (NKu) (Nama Karoo Biome).

Assessment rationale: EOO = 988 530 km^2; AOO would be smaller, but, nevertheless, widespread across sandy regions; much of range lies in little-transformed areas used primarily for grazing of domestic livestock to which the species is readily attracted; despite some taxonomic uncertainty, assessed as Least Concern (LC) as no populations apparently face threats.

Conservation measures: Resolution of Group 22 taxonomic uncertainties is required to improve assessment of conservation status; protected in Kgalagadi Transfrontier Park and Kruger National Park (Botswana, South Africa).

Onthophagus corniculiger

d'Orbigny, 1913



No synonyms

Global: DD

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Afrique orientale portugaise: Zambézie' [Zambezia Province, central Mozambique].

Taxonomy: Accepted Group 12 species (subgenus: *Trichonthophagus*), but described from a single specimen; should be compared to type material of *O. decedens* Péringuey, 1904, (not located) described from 'Southern Rhodesia (Sebakwe)' [Zimbabwe]; like most Group 12 species *O. corniculiger* is sexually dimorphic (head, prothoracic disc); as characters show great morphological variability according to body size, a review of the group taxonomy would be useful.

Distribution: Most known records from reserves in moist savanna on the S Mozambique Coastal Plain (Mozambique, South Africa), but also from bushveld in NW South Africa; citation from Zambia requires validation.

Locality data (mean ± SD, range): Altitude: 450 ± 402, 55–1 448 m; annual rainfall: 629 ± 120, 435–900 mm; annual temperature (max. + min. /2): 21.7 ± 1.7, 18.2–23.6°C (N=14).

Habitat: No quantitative assessment; sampled in small numbers on both sandy granite-derived and finer gabbro-derived soils in very open woodland at South African Wildlife College (Kruger National Park).

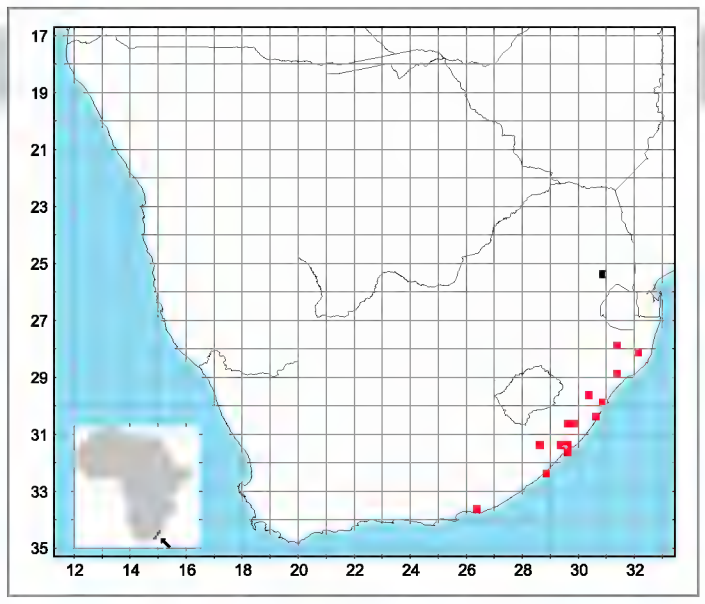
Food types: No quantitative assessment; DBRU collection records all from elephant dung (4).

Temporal activity: Diel flight periodicity unknown, but probably in darkness like some other Group 12 species; recorded during the summer rainy season (Nov. to Mar.).

Bioregions South Africa: Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 145 035 km² (gross estimate); AOO would be much smaller owing to specialisation to dung of large monogastric herbivores whose range is severely contracted within SE Africa; elephants remain protected across circa 20% of the putative range for *O. corniculiger*; unclear if AOO would also be influenced by habitat associations as these are essentially unknown; currently assessed as Data Deficient (DD).

Conservation measures: Conservation of this species would be dependent on protection of elephants; to adequately assess conservation status, the current EOO and AOO need to be more precisely determined by a survey of elephant dung in game reserves of SE Africa; quantitative data on habitat associations is also required; protected in Kruger National Park, uMkhuze and Hluhluwe–iMfolozi game reserves (South Africa).



Onthophagus cretus

Péringuey, 1901

See Taxonomy section.

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'Natal (Durban, Umkomas River)' [Durban, KwaZulu-Natal, South Africa]; Also 'Ovampoland (Humbe)' [Ovamboland, Namibia – considered an error].

Taxonomy: Group 23 species currently synonymised with *Onthophagus setosus* Fahraeus, 1857, described from 'prope fluvium Limpopo' [near Limpopo River]; this type locality lies outside of the range of the species treated here as *O. cretus*, which may, therefore, deserve revalidation as a 'bona fide' species; however, further study required; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.

Distribution: Primarily SE coastal and SE lower escarpment forest patches in South Africa; validated as same species (red squares), tentative (black square).

Locality data (mean ± SD, range): Altitude: 586 ± 459, 0–1 431 m; annual rainfall: 876 ± 111, 482–1 015 mm; annual temperature (max. + min. /2): 18.0 ± 1.8, 14.2–20.5°C (N=21).

Habitat: No quantitative assessment; 78.6% (22) of available records (28) cited from forest; no soil type records.

Food types: No quantitative assessment; no records.

Temporal activity: Diel flight periodicity unknown; active primarily during the summer rainy season (Aug. to Apr.).

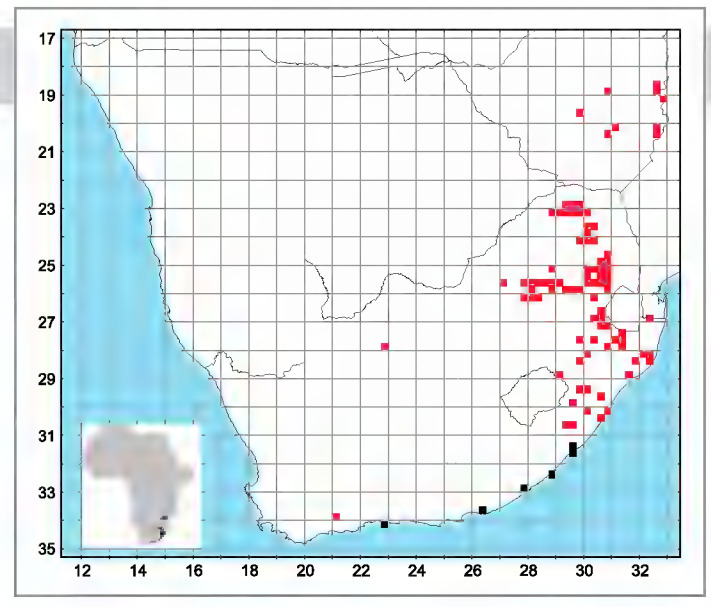
Bioregions South Africa: Locality records primarily from patches of Southern Mistbelt Forest (FOz 3) and Scarp Forest (FOz 5) within the Indian Ocean Coastal Belt Biome (CB) and E edge of Grassland Biome (G).

Assessment rationale: EOO = 44 150 km^2; AOO would be much smaller due to forest patch specialisation; often comparatively abundant; within reserves, FOz 3 and FOz 5 are assessed as least threatened although uncontrolled exploitation is a problem; *O. cretus* is currently assessed as Least Concern (LC) owing to widespread occurrence in many forest reserves.

Conservation measures: Taxonomic issues of species validity need to be resolved. Assessment of conservation status would be improved by quantitative data on ecological associations, particularly food and soil type; protected in various forest reserves, including Dwesa, Ntsubane and Silaka (Eastern Cape).

Onthophagus cribripennis

d'Orbigny, 1902



No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Afrique austral: Zoulouland' [Zululand, South Africa].

Taxonomy: Accepted Group 17 species, but populations recorded primarily in forest along SE coast require re-assessment (black squares); male aedeagus of these populations identical to typical *O. cribripennis*, but ridge on vertex of female somewhat arcuate rather than straight; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.

Distribution: Primarily warm, moist woodland savanna and forest plus moist coastal and upland grasslands of SE Africa: South Africa, Mozambique, Zimbabwe; also cited from Malawi.

Locality data (mean ± SD, range): Altitude: 1 122 ± 521, 0–2 286 m; annual rainfall: 800 ± 162, 305–1 659 mm; annual temperature (max. + min. /2): 17.5 ± 2.2, 10.6–22.7°C (N=146).

Habitat: At 13–1 400 m on Wolkberg: more abundant in forest (21.1) than grassland (2.7); at Carolina in Dec.: more abundant in improved Kikuyu pasture (25.8) and regenerating vegetation of fallow crop fields (12.7) than in natural *Themeda* grassland (4.9); DBRU collection records suggest a bias to finer-grained soils (sand: 6, sandy loam: 17, sandy clay loam: 28, clay: 4) although most recorded in pasture/grassland (43) or forest (8), also shrub/woodland (5).

Food types: At 13–1 400 m on Wolkberg: more abundant on pig dung (16.2) than cattle dung (7.6); DBRU collection records primarily from dung of cattle (50), also baboon (1), human (1), human/cattle or buffalo mix (8), rhinoceros (1), zebra (1).

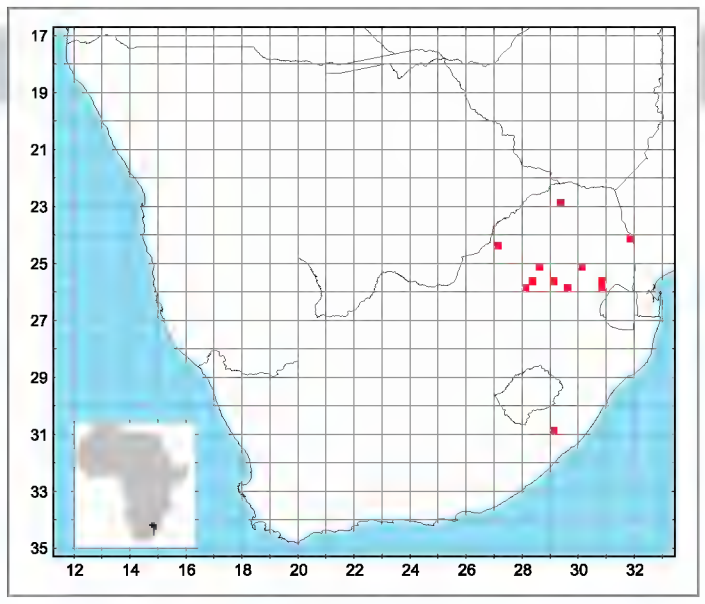
Temporal activity: Diurnal flight activity during much of the year (Aug. to May).

Ecoregions Zimbabwe: Primarily Southern Miombo Woodlands (AT0719), Eastern Zimbabwe Grassland Forest Mosaic (AT1006).

Bioregions South Africa: Straddling edges of Central Bushveld (SVcb) and Lowveld (SVl) in Soutpansberg and Waterberg (Savanna Biome); N and E edges of Mesic Highveld Grassland (Gm), N Sub-Escarpment Grassland (Gs) (Grassland Biome); Indian Ocean Coastal Belt Biome (CB); warmer S coast forest patches.

Assessment rationale: EOO = 206 820 km^2; AOO may be influenced by soil type bias, but quantitative support required; comparatively widespread and abundant in both reserves and farm rangeland; abundance apparently greater in improved pasture than in natural grassland; therefore, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by further quantitative ecological data to determine soil associations and resolve conflicts in vegetation and dung associations; protected in Ithala and Hluhluwe–iMfolozi game reserves (South Africa).



Onthophagus croesulus

Bates, 1888

= *Onthophagus obtusicollis* Péringuey, 1888

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. croesulus*: 'Natal' [KwaZulu-Natal, South Africa]; *O. obtusicollis*: 'Potchefstroom and Pretoria, Transvaal' [South Africa: North-West Province and Gauteng].

Taxonomy: Accepted Group 18 species; limited sexual dimorphism (head, prothoracic disc) varying in prominence with body size.

Distribution: Patchy records from moist savanna and grasslands in N and E South Africa; patchiness probably a collection artefact due to dietary specialisation.

Locality data (mean ± SD, range): Altitude: 1 113 ± 323, 305–1 553 m; annual rainfall: 680 ± 132, 525–1 022 mm; annual temperature (max. + min. /2): 18.4 ± 2.1, 15.4–22.5°C (N=13).

Habitat: No quantitative assessment; sampled in open woodland on koppies in Telperion Nature Reserve (2); one DBRU collection record from sandy clay loam in grassland.

Food types: No quantitative assessment; sampled to pig dung bait in Telperion Nature Reserve (2); one DBRU collection record from a dead millipede.

Temporal activity: Diurnal flight activity in the summer rainy season (Oct. to Mar.).

Bioregions South Africa: Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome); N and E edges, Mesic Highveld Grassland (Gm) (Grassland Biome) adjoining the savanna bioregions; also E edge, Sub-Escarpment Grassland (Gs) adjoining Sub-Escarpment Savanna (SVs).

Assessment rationale: EOO = 128 590 km^2; no quantitative data, but probably a carrion specialist like other members of Group 18 *Onthophagus*; recorded over a wide range including in grassland where carrion would be readily available; probably not threatened, however, ecologically poorly known, so assessed as Data Deficient (DD).

Conservation measures: Before an assessment may be made of conservation status, quantitative data on ecological associations are required; it is also necessary to conduct a survey to determine the full EOO and AOO; protected in Nascott and Telperion nature reserves.

Onthophagus cupricollis

Péringuey, 1888

No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Lydenburg, Transvaal' [Mashishing, Mpumalanga, South Africa].

Taxonomy: Accepted Group 18 species; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.

Distribution: South Africa: moist upland savanna on Waterberg (Limpopo and Mpumalanga provinces) and NE escarpment.

Locality data (mean ± SD, range): Altitude: 1 228 ± 296, 603–1 627 m; annual rainfall: 762 ± 127, 563–1 022 mm; annual temperature (max. + min. /2): 17.6 ± 2.0, 14.7–20.7°C (N=11).

Habitat: Not known.

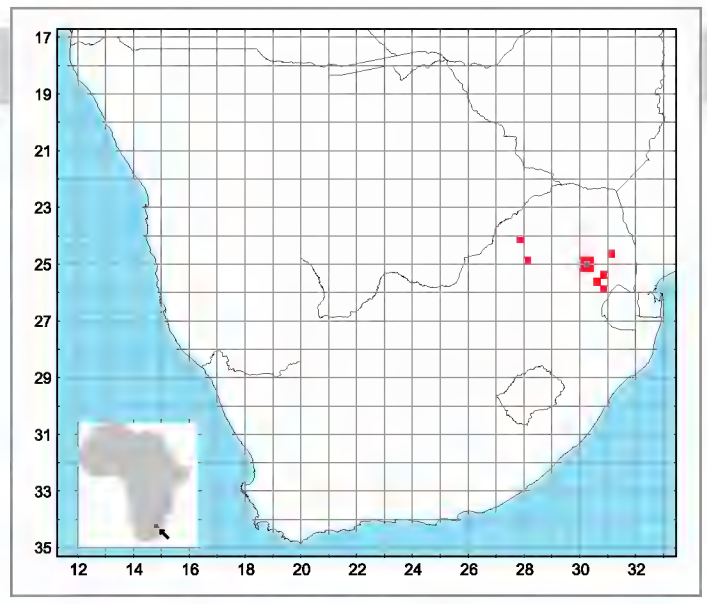
Food types: No quantitative assessment; trapped to meat bait.

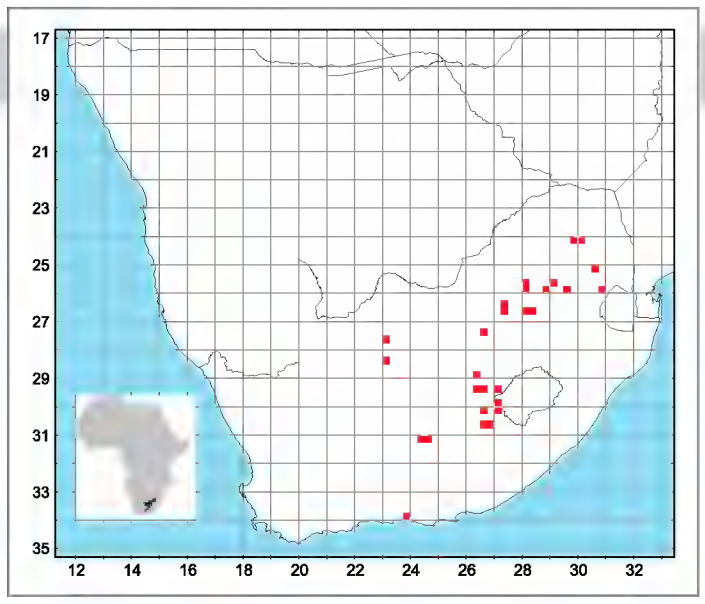
Temporal activity: Attracted to light, so presumably flies in darkness; recorded primarily in the summer rainy season (Oct. to Mar.).

Bioregions South Africa: Moist uplands of Central Bushveld (SVcb) and Lowveld (SVl) (Savanna Biome) plus NE extremity of Mesic Highveld Grassland (Gm) (Grassland Biome).

Assessment rationale: EOO = 26 645 km^2; poorly known, but attraction to meat bait suggests carrion associations like other close relatives in Group 18; AOO may be restricted to moist savanna regions of central N South Africa, but range probably somewhat underestimated; currently assessed as Data Deficient (DD).

Conservation measures: Before an assessment of conservation status may be made, a quantitative survey is required to determine the full EOO, AOO and ecological associations; the survey should be centred on moist upland savanna along the Waterberg and NE escarpment; protected in Mabalingwe Game Reserve and Nelspruit Nature Reserve.





Onthophagus cyaneoniger

d'Orbigny, 1902

No synonyms

Global: LC (see IUCN Red List – LC)
Endemic: RSA (but see Distribution)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'Transvaal: Hamman's Kraal près de Pretoria..... Bechouana: Vryburg.....; État d'Orange: Bloemfontein....; Natal' [South Africa: Hammanskraal, Vryburg, Bloemfontein, KwaZulu-Natal].

Taxonomy: Accepted Group 23 species; sexually dimorphic (head), characters vary in prominence with body size.

Distribution: Centred on the grasslands of the South African Highveld with peripheral records in the Northern Cape, highlands of Upper Karoo and transformed Eastern Cape coastal habitat; disjunct pattern may reflect soil specialisation, a collection artefact related to small body size, or both; citations from Botswana, Zimbabwe, Democratic Republic of the Congo (DRC) require validation as they are likely errors.

Locality data (mean ± SD, range): Altitude: 1 411 ± 240, 290–1 860 m; annual rainfall: 590 ± 168, 308–1 022 mm; annual temperature (max. + min. /2): 16.1 ± 1.5, 13.2–19.5°C (N=42).

Habitat: No adequate quantitative assessment, but recorded in abundance in grassland on sand (24.3/sample, Telperion NR) and sandy loam (65.0/sample, Abe Bailey NR), but uncommon on sandy clay loam (0.5/sample, Suikerbosrand NR); DBRU collection records on sand (1), sandy loam (6), sandy clay loam (1) in grassland/pasture (6), also fallow crop field (1).

Food types: No quantitative assessment; sampled to pig dung and to combined sheep/cattle dung bait; DBRU collection records exclusively on cattle dung (13).

Temporal activity: Diel flight periodicity unknown, but probably diurnal; active in the summer rainy season (Oct. to May).

Bioregions South Africa: Dry Highveld Grassland (Gh), Mesic Highveld Grassland (Gm) (Grassland Biome), E Upper Nama Karoo (NKu) (Nama Karoo Biome); also in Eastern Kalahari Bushveld (SVk) (Savanna Biome).

Assessment rationale: EOO = 181 630 km^2; AOO may be smaller due to possible bias to sandier soils although this requires rigorous quantitative support as the data cited above might be influenced by climate; range is subject to extensive transformation, but recorded in cattle dung on farms over a wide range; also abundant in some Highveld nature reserves; assessed as Least Concern (LC).

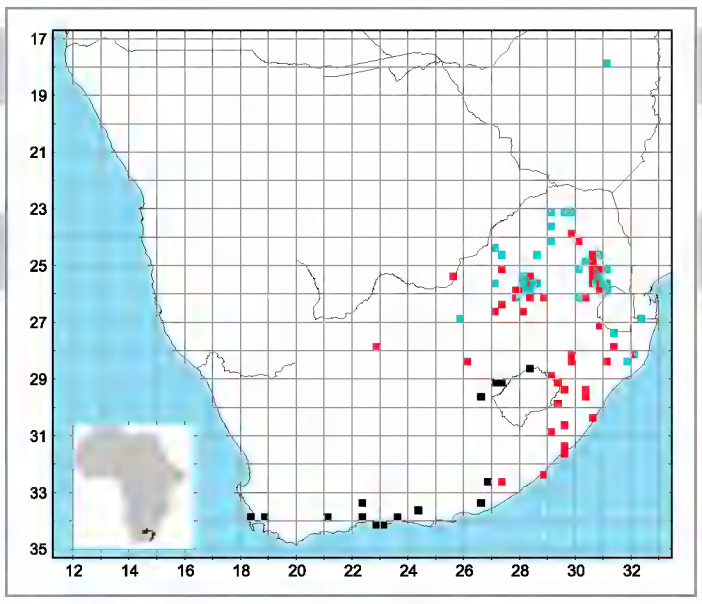
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, including effects of pasture improvement or habitat modification; protected in Telperion, Suikerbosrand, Abe Bailey nature reserves (Gauteng).

Onthophagus deterrens

Péringuey, 1901

Onthophagus variolosus

d'Orbigny, 1902



No synonyms

Global: DD
Endemic: RSA (but see Taxonomy section)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. deterrens*: 'Cape Colony (Stellenbosch, in carrion; Paarl), Natal (Durban), Transvaal (Lydenburg), Southern Rhodesia (Salisbury)' [South Africa; Zimbabwe]; *O. variolosus*: 'Colonie du Cap: Cape Town' [Cape Town, Western Cape, South Africa].

Taxonomy: Both accepted Group 19 species, but status needs validation or revision after comparison between types; as aedeagi are identical, *O. variolosus* may be a junior synonym and blue colour variety of metallic green, *O. deterrens*; cited type localities for *O. deterrens* (SW Cape to Zimbabwe) suggest inclusion of two or three species; in two, the vertex of females bears a spine (*O. deterrens, O. variolosus*), in one, it bears a ridge (*Onthophagus* sp. nr *deterrens*).

Distribution: *O. variolosus* (black squares): S Cape and NW Lesotho border, South Africa; *O. deterrens* (red squares): NE Highveld and E coast, South Africa; *O.* sp. nr *deterrens* (turquoise squares): N savanna, South Africa to Zimbabwe.

Locality data (mean ± SD, range): *O. variolosus*: altitude: 820 ± 630, 26–1 830 m; annual rainfall: 519 ± 150, 270–879 mm; annual temperature (max. + min. /2): 15.7 ± 1.6, 13.3–17.8°C (N=16). *O. deterrens*: altitude: 1 275 ± 463, 28–2 274 m; annual rainfall: 793 ± 156, 338–1 271 mm; annual temperature (max. + min. /2): 16.6 ± 2.1, 10.6–20.5°C (N=55). *O.* sp. nr *deterrens*: altitude: 1 119 ± 386, 58–1 746 m; annual rainfall: 719 ± 115, 533–1 013 mm; annual temperature (max. + min. /2): 18.4 ± 1.8, 14.0–22.6°C (N=42).

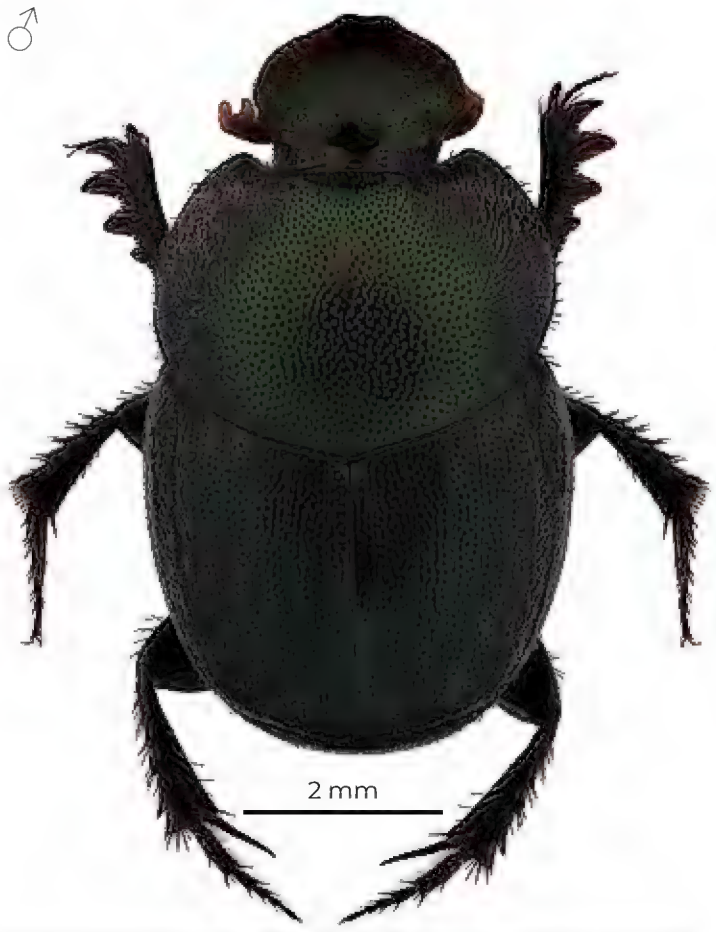
Habitat: No quantitative assessment; limited DBRU records for species complex from finer-grained soils: sandy loam (1), sandy clay loam (2) in pasture/grassland (2).

Food types: No quantitative assessment; limited DBRU records for species complex from carnivore dung (dog; 2) or dead animals (toad, millipede and tenebrionid beetle; 3).

Temporal activity: Diel flight periodicity unknown; species complex active throughout summer rainy season (Sept. to Apr.).

Bioregions South Africa: *O. variolosus*: S Mesic Highveld Grassland (Gm) (Grassland Biome), mainly Renosterveld vegetation units (Fynbos Biome); *O. deterrens*: primarily Sub-Escarpment Grassland (Gs) in SE plus N and NE edge of Mesic Highveld Grassland (Gm) (Grassland Biome), also Indian Ocean Coastal Bet Biome (CB); *O.* sp. nr *deterrens*: primarily Central Bushveld (SVcb) and moister S and W of Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 58 525 km², 293 240 km², 111 545 km², respectively, *O. variolosus*, *O. deterrens*, *O.* sp. nr *deterrens*; owing to localities cited in original description any one of the three could be the 'real' *O. deterrens*; thus, impossible to assess conservation status although wide range and association with carnivore dung or carrion



O. deterrens

O. deterrens

Onthophagus deterrens & *O. variolosus* (continued)

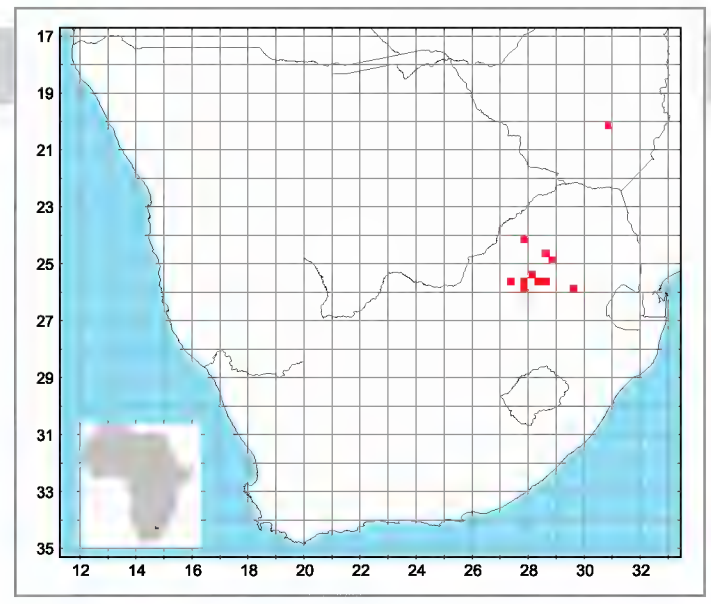
O. variolosus

suggests no member of the species complex is threatened; currently assessed as Data Deficient (DD).

Conservation measures: Uncertainties in species status and nomenclature need to be resolved before conservation status may be assessed; quantitative data on ecological associations are also required; protected in various nature reserves: Coleford, Abe Bailey, Suikerbosrand (*O. deterrens*); Roodeplaat, Rustenburg (*O.* sp. nr *deterrens*).

Onthophagus discretus

Péringuey, 1901



No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Transvaal (Rustenburg)' [Rustenburg, North-West Province, South Africa].

Taxonomy: Accepted Group 7 species; minor sexual dimorphism (head).

Distribution: Disjunct, scattered pattern in SE Africa owing to specialisation to moist, shaded, upland vegetation: South Africa, Zimbabwe; also cited from Malawi.

Locality data (mean ± SD, range): Altitude: 1 166 ± 158, 973–1 553 m; annual rainfall: 648 ± 51, 563–745 mm; annual temperature (max. + min. /2): 19.0 ± 1.5, 15.4–21.9°C (N=13).

Habitat: In Gauteng bushveld: recorded on both deep sand (13) and sandy clay loam (36), but with extreme bias to shaded thickets (49) compared to open woodland (0) and grassland (0); similar at Roodeplaat Nature Reserve on sandy clay loam: shaded thicket (12), open woodland (1), grassland (0); a single DBRU collection record from shaded *Brachystegia* forest.

Food types: No quantitative assessment; a single DBRU collection record from human/cattle dung mix.

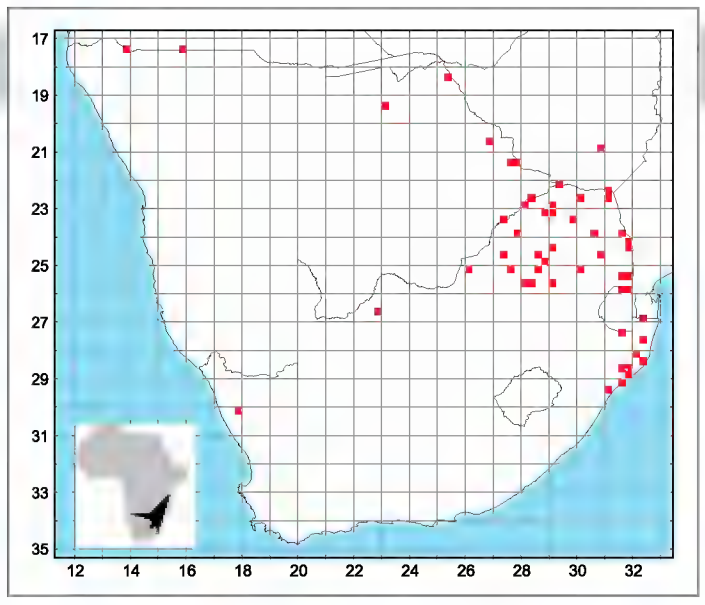
Temporal activity: Flight activity in darkness during the summer rainy season (Oct. to Mar.); in Gauteng bushveld: peak activity early to mid-rainy season (Oct. to Dec.).

Ecoregions Zimbabwe: Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Primarily Central Bushveld (SVcb) (Savanna Biome).

Assessment rationale: EOO = 42 255 km^2 (underestimated); AOO much smaller owing to association with shaded thicket and dense woodland; would be susceptible to clearance of dense woody vegetation although also recorded in eucalypt plantation; transformation in vegetation units of known range in South Africa, 3–49%; currently assessed as Least Concern (LC) pending further research.

Conservation measures: Assessment of conservation status would be improved by a survey of the surviving dense woody vegetation in upland SE Africa to better determine the EOO, AOO as well as dung type associations on both deep sand and finer-grained soils; protected in Roodeplaat and Nascott nature reserves (South Africa), Lake Mutirikwe Game Reserve (Zimbabwe).



Onthophagus ebenicolor

d'Orbigny, 1902

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'Afrique orientale allemande...., Zambèze' [Tanzania; ?N Mozambique].

Taxonomy: Accepted Group 19 species, but distribution data requires validation owing to a number of putative close relatives of similar appearance; sexually dimorphic (head), character varies in prominence with body size.

Distribution: Dry to moist savanna from southern to E Africa: South Africa, Namibia, Botswana, Zimbabwe, Mozambique, Zambia, Tanzania; also reported from Kenya.

Locality data (mean ± SD, range): Altitude: 716 ± 445, 1–1 850 m; annual rainfall: 619 ± 205, 162–1 177 mm; annual temperature (max. + min. /2): 20.8 ± 2.0, 13.4–25.2°C (N=69).

Habitat: No quantitative assessment; limited DBRU collection records on sand (1), sandy clay loam (2), clay (2) in pasture (1), shrub/woodland (4) or forest (1).

Food types: No quantitative assessment; limited DBRU collection records on gut content of impala (2), human/buffalo or cattle dung mix (2); also dung of buffalo (1) or cattle (1); also see Assessment rationale.

Temporal activity: Flight activity in darkness, primarily during the summer rainy season (Oct. to May); attracted to light.

Ecoregions Namibia, Botswana, Zimbabwe: Namibian Savanna Woodlands (AT1316), Angolan Mopane Woodlands (AT0702), Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian and Mopane Woodlands (AT0725), Southern African Bushveld (AT0717).

Bioregions South Africa: Central Bushveld (SVcb), Lowveld (SVl), Mopane (SVmp) (Savanna Biome); Indian Ocean Coastal Belt Biome (CB); single records in two other ecoregions.

Assessment rationale: EOO = 1 691 195 km^2; AOO unclear; ecologically poorly known owing to lack of quantitative data, but Group 19 is thought to be characterised primarily by carrion associations; habitat associations possibly biased to finer-grained soils and woody vegetation; however, probably widespread; therefore, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status needs to be improved by quantitative ecological data to confirm bias in habitat associations and bias in food associations with omnivore dung and/or carrion specialisation; protected in Kruger National Park (South Africa).

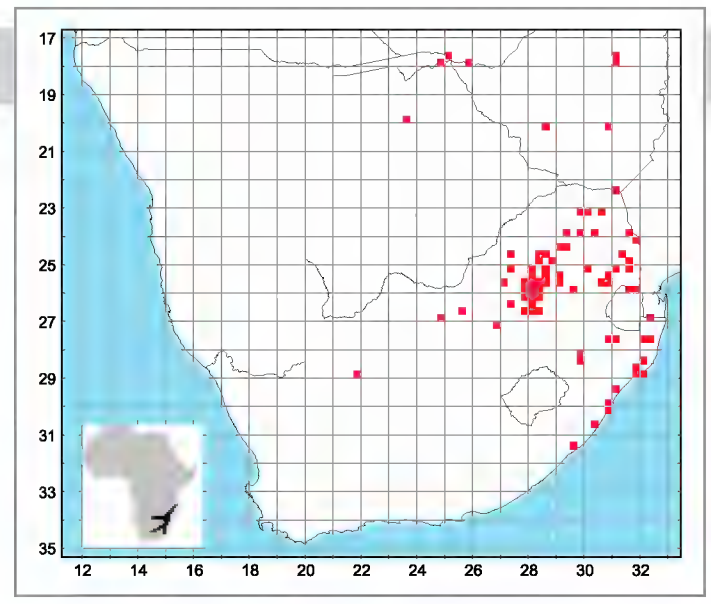
Onthophagus ebenus

Péringuey, 1888 (but see Taxonomy)

= *Onthophagus natalicus* d'Orbigny, 1902

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: *O. ebenus*: 'From the banks of the Vaal River' [inexact, Vaal River, N South Africa]; *O. natalicus*: 'Natal...: Durban....; Transvaal: Makapan près de Pietersburg' [South Africa: Durban and Makapan, KwaZulu-Natal and Limpopo provinces].

Taxonomy: Accepted Group 24 species; sexually dimorphic (head prothoracic disc), characters vary in prominence with body size; subsequent to completion of the manuscript for this book, this Group 24 species was placed in a new genus, *Tiaronthophagus* Roggero, Moretto, Palestrini & Barbero, 2019, comprising 26 species from three different groups.

Distribution: Moist coastal and upland open savanna in SE Africa: South Africa, N Botswana, Zimbabwe, Mozambique; also reported from Malawi, SE Tanzania.

Locality data (mean ± SD, range): Altitude: 953 ± 522, 0–1 824 m; annual rainfall: 704 ± 147, 205–1 254 mm; annual temperature (max. + min. /2): 19.3 ± 2.2, 14.2–25.2°C (N=123).

Habitat: No clear soil specialisation in Gauteng bushveld: deep sand (5), sandy clay loam (11), or in uMkhuze Game Reserve: sand (0.1), sand over clay (0.3), sandy clay loam (0.8), clay (0.3); at Roodeplaat Nature Reserve: bias to open vegetation, grass (32), open woodland (20), shaded thicket (2); limited DBRU collection records on sand (1), sandy loam (3), sandy clay loam (3), clay (1).

Food types: In Gauteng bushveld: extreme bias to omnivore dung (pig, 12) and carrion (14) compared to dung of ruminant herbivore (cattle, 0) and monogastric herbivore (horse, 0); bias supported by limited DBRU collection records from human/cattle or buffalo dung mix (5), cattle dung (3).

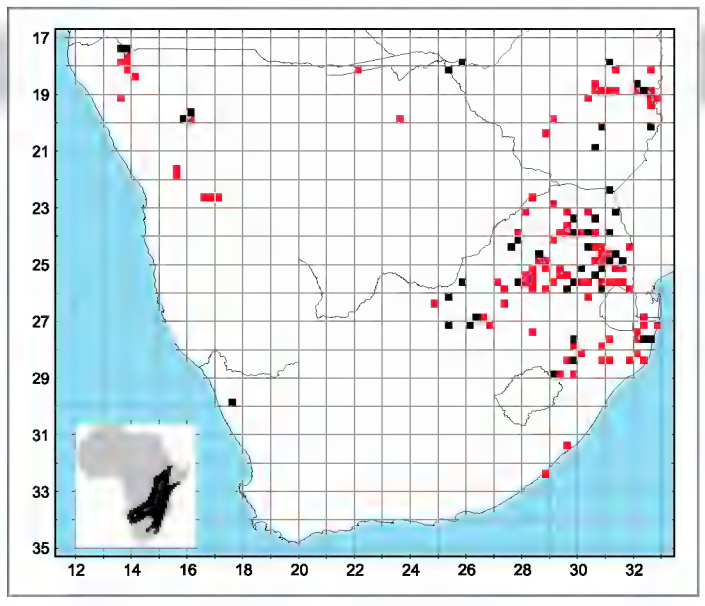
Temporal activity: Flight activity in darkness; recorded during most months of the year (Aug. to May) although primarily active during the summer rainy season (Oct. to Mar.); attracted to light.

Ecoregions Botswana, Zimbabwe: Zambezian and Mopane Woodlands (AT0725), Southern African Bushveld (AT0717), Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Primarily Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome) and Indian Ocean Coastal Belt Biome (CB); also N margins of Grassland Biome (3 bioregions).

Assessment rationale: EOO = 847 490 km²; widespread omnivore dung and carrion specialist showing a bias to open vegetation; possibly tolerant of urbanisation as it has been recorded on dog dung in Pretoria city suburbs; therefore, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by stronger data to support soil generalisation or a slight bias to finer-grained soils; protected in Kruger National Park, Leeuwfontein and Abe Bailey nature reserves (South Africa).



Onthophagus fimetarius

Roth, 1851

= *Onthophagus piceus* Fahraeus, 1857
= *Onthophagus lugens* Fahraeus, 1857, *sensu* Péringuey, 1901

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. fimetarius*: 'Abyssinien' [inexact, Ethiopia]; *O. piceus*: 'prope fluvium Limpopo' [near Limpopo River, southern Africa]; *O. lugens sensu* Péringuey: 'Cape Colony (Kimberley), Natal (Newcastle, Frere, Durban), Transvaal (Potchefstroom, Rustenburg), Southern Rhodesia (Salisbury, Upper Hanyani River, Victoria Falls)' [South Africa, Zimbabwe].

Taxonomy: Accepted Group 23 species, but revision required as species of similar appearance have been variously synonymised or revalidated by past researchers; synonymy of southern African *O. piceus* with Ethiopian *O. fimetarius* requires further validation; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.

Distribution: Cited from savanna throughout the Afrotropical region: single species composition validated by extraction of aedeagi for South Africa, Namibia, Angola, Zimbabwe, Mozambique, Malawi, Tanzania, Kenya (black squares on map); also cited from Lesotho, Eswatini, Botswana, Democratic Republic of the Congo (DRC), Uganda, Sudan, Somalia, Ethiopia, Eritrea and 15 W African countries.

Locality data (mean ± SD, range): Altitude: 1 069 ± 453, 0–2 286 m; annual rainfall: 683 ± 198, 120–1 415 mm; annual temperature (max. + min. /2): 18.8 ± 2.4, 10.6–24.8°C (N=199).

Habitat: On Gauteng bushveld: strong bias to deep sand (1 385) compared to sandy clay loam (221), but a vegetation generalist (grassland: 491, open woodland: 563, shaded thickets: 532); at Carolina in Jan.: much more abundant in natural *Themeda* grassland (71) compared to regenerating vegetation of fallow crop fields (10) or improved Kikuyu grass pasture (8); DBRU collection records from sand (19), sandy loam (28), sandy clay loam (19), clay (4) in pasture/grassland (45), shrubland/open woodland (32), shaded thicket (1),

Food types: On Gauteng bushveld: primarily attracted to omnivore dung (pig: 73), but also to herbivore dung (cattle: 29, horse: 15), rarely to carrion (2); DBRU collection records on dung of cattle (70), wildebeest (2), elephant (1), human (1), human/buffalo or cattle mix (6).

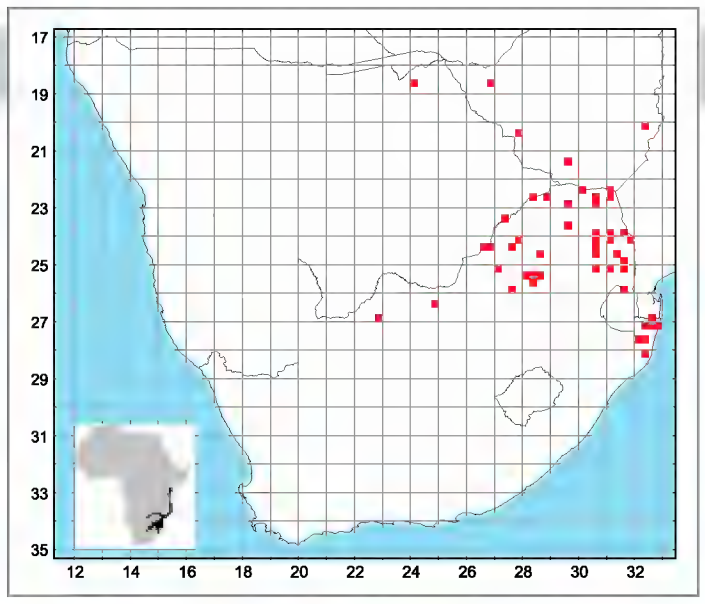
Temporal activity: Flight activity during darkness in the summer rainy season (Aug., Oct. to May); on Gauteng bushveld: primarily active in early summer (Oct. to Dec.) tailing off from mid-summer into early winter (Jan. to May); also on Gauteng bushveld: flies primarily early evening (18:00–20:00) in early (Nov.) and late summer (Feb., Mar.), but also at dawn in warmer mid-summer (Jan., 04:00–06:00), attracted to light.

Ecoregions Namibia, Botswana, Zimbabwe: N Namibian Savanna Woodlands (AT1316), Kalahari Xeric Savanna (AT1309), Angolan Mopane Woodlands (AT0702), Zambezian and Mopane Woodlands (AT0725), Zambezian Baikiaea Woodlands (AT0726), Southern African Bushvelld (AT0717), Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome); N Grassland Biome (Dry Highveld Grassland (Gh), Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs)); Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 5 546 895 km² (gross estimate based on range from S to NE Africa); extremely wide range with generalist vegetation associations; possible soil bias and intolerance of habitat disturbance requires further validation, assessed as Least Concern (LC).

Conservation measures: Taxonomic revision is required to validate nomenclature used for a species that is ecologically well known in N South Africa; protected in many reserves including Kruger National Park (South Africa), Serengeti National Park (Tanzania).



Onthophagus flavolimbatus

Klug, 1855

= *Onthophagus bicolor* Raffray *sensu* d'Orbigny, 1900
= *Onthophagus semiflavus* Boheman, 1857, *sensu* d'Orbigny, 1902
= *Onthophagus breviculus* d'Orbigny, 1905

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. flavolimbatus*: 'Sena' [central Mozambique]; *O. bicolor sensu* d'Orbigny: 'Afrique allemande orientale: Bagamoyo' [Tanzania]; *O. semiflavus sensu* d'Orbigny: 'Transvaal' [South Africa]; *O. breviculus*: 'Transvaal: Hamman's Kraal' [Hammanskraal, South Africa].

Taxonomy: Accepted Group 11 species; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.

Distribution: Mostly, dry, lower-altitude savanna on the E seaboard from S to E Africa: South Africa, N Botswana, Zimbabwe, Mozambique, Kenya, Tanzania.

Locality data (mean ± SD, range): Altitude: 620 ± 419, 5–1 670 m; annual rainfall: 627 ± 180, 304–1 275 mm; annual temperature (max. + min. /2): 21.3 ± 1.9, 14.5–25.7°C (N=72).

Habitat: In Gauteng bushveld: bias to coarse-grained soils in open vegetation, sand (462), sandy clay loam (64), grassland (267), open woodland (254), shaded thicket (5); in uMkhuze Game Reserve: similar bias, sand (3.1), sand on clay (6.1), sandy clay loam (0.1), clay (1.3); DBRU collection records less supportive, sand (8), sandy loam (10), sandy clay loam (7), clay (2) in pasture (2), shrubland (7), open woodland (17).

Food types: Relative dung generalist in Gauteng bushveld, but lower on monogastric herbivore dung: cattle (30), horse (19), pig (29), carrion (1); similar at Phalaborwa: pig (1 001), cattle (1 061), elephant (351); DBRU collection records from dung of cattle (20), buffalo (1), wildebeest (1), elephant (1), horse (1), donkey (2), human/cattle mix (2).

Temporal activity: Diurnal flight activity; in Gauteng bushveld: peaking between 10:00–14:00 (Nov. to Feb.), tailing off to 16:00; active in the summer rainy season (Oct. to Apr.); in Gauteng bushveld: peaking Oct. to Feb., tailing off early Mar.; at Phalaborwa: more abundant in warm sunny conditions after heavy rainfall (1 391) than in hot, sunny, dry conditions (794), or warm cloudy conditions after light rainfall (55).

Ecoregions Botswana, Zimbabwe: Kalahari Acacia-Baikiaea Woodands (AT0709), Southern African Bushveld (AT0717), Zambezian and Mopane Woodlands (AT0725).

Bioregions South Africa: Eastern Kalahari Bushveld (SVk), Central Bushveld (SVcb), Lowveld (SVl), Mopane (SVmp) (Savanna Biome); also N Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 860 785 km^2 (gross estimate); AOO possibly smaller due to sandy soil bias; however, widespread in both grassland and wooded habitats where it shows relatively generalist dung associations; assessed as Least Concern (LC).

Conservation measures: None required; protected in various reserves including Kruger National Park, uMkhuze Game Reserve (South Africa), Gorongosa National Park (Mozambique).

Onthophagus fritschi

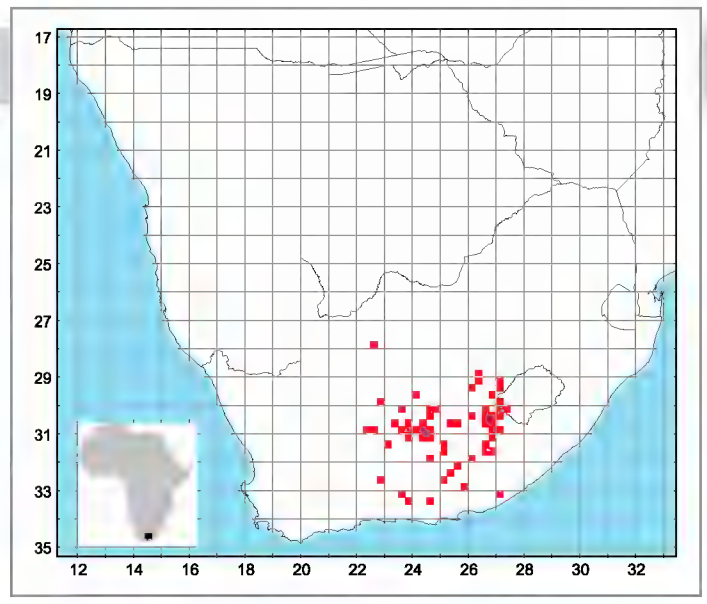
d'Orbigny, 1902

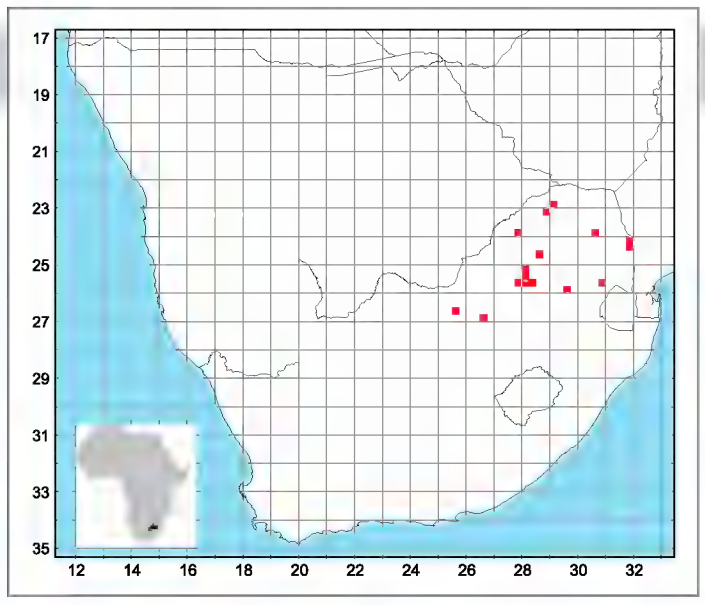
No synonyms

Global: LC
Endemic: RSA (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Afrique australe' [southern Africa].
Taxonomy: Accepted Goup 31 species (subgenus *Furconthophagus*); sexually dimorphic (head), characters vary greatly in prominence with body size.
Distribution: Mostly dry upland Karoo and grassland of central South Africa and lower-altitude, dry areas inland from the S coast.
Locality data (mean ± SD, range): Altitude: 1 333 ± 292, 210–2 199 m; annual rainfall: 413 ± 142, 221–741 mm; annual temperature (max. + min. /2): 15.4 ± 1.3, 11.2–18.6°C (N=80).
Habitat: No adequate quantitative data; in Northern Cape: almost exclusively in Upper Karoo (frequency: 45.6%; 31 out of 68 samples), soil data inconclusive: sand (10.2 per sample, N=18), sandy loam (5.6, N=11) but 173.8 per sample in a moist, outlier clay vlei at arid W margins of range; DBRU collection data from sand (8), sandy loam (15), sandy clay loam (10), clay (3) in grassland/pasture (17), scrub/shrubland (9).
Food types: No quantitative data; DBRU collection records primarily from dung of cattle (43), also sheep (1), donkey (1), zebra (1), human/cattle mix (1).
Temporal activity: Diel flight periodicity unknown, but presumably diurnal activity in summer rainy season (Oct. to May).
Bioregions South Africa: Centred on S Dry Highveld Grassland (Gh) and SW margins of three other bioregions (Grassland Biome); also Upper Karoo (NKu), Lower Karoo (NKl) (Nama Karoo Biome) and Albany Thicket Biome (AT).
Assessment rationale: EOO = 174 610 km²; available data suggest a soil generalist in open grassland and open shrubland vegetation, but quantitative support required; widely recorded from dung of farm livestock across a range that is little transformed to the W and only 10–12% transformed to the NE; currently assessed as Least Concern (LC).
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations and more precise measurement of EOO as regards E edge of range, which approaches the range of the very closely related *O. lamnifer* d'Orbigny, 1902; not currently known from any protected area.





Onthophagus fugitivus

Péringuey, 1901

No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Transvaal (Klerksdorp)' [North-West Province, South Africa].

Taxonomy: Accepted Group 31 species (subgenus *Furconthophagus*); sexually dimorphic (head), characters vary in prominence with body size.

Distribution: Uplands and adjoining lowlands, N South Africa; patchy occurrence possibly related to soil specialisation; record from Botswana requires validation.

Locality data (mean ± SD, range): Altitude: 1 042 ± 372, 286–1 553 m; annual rainfall: 607 ± 84, 422–801 mm; annual temperature (max. + min. /2): 19.2 ± 1.9, 15.4–22.5°C (N=18).

Habitat: No quantitative assessment; limited DBRU collection records from sandy clay loam (1) or clay (1) in shrubland (1) or woodland (1); long series from Nylsvlei (Ditsong Museum), all but one collected near a river, which may indicate alluvial soils rather than sand.

Food types: No quantitative assessment; limited DBRU collection records from cattle dung (2).

Temporal activity: Diel periodicity not known; active in the summer rainy season (Oct. to Apr.).

Bioregions South Africa: Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome); N Dry Highveld Grassland (Gh), N Mesic Highveld Grassland (Gm) (Grassland Biome).

Assessment rationale: EOO = 118 900 km^2; AOO probably much smaller, but poorly known ecologically; AOO may be influenced by specialised soil association, but quantitative support required; probably no bias in association with open or partially shaded vegetation, but quantitative support is lacking; although probably not threatened due to extensive EOO, currently assessed as Data Deficient (DD).

Conservation measures: Quantitative data on ecological associations are required before an assessment may be made of conservation status; protected in Roodeplaat and Mogol nature reserves, also on Satara Floodplain in Kruger National Park.

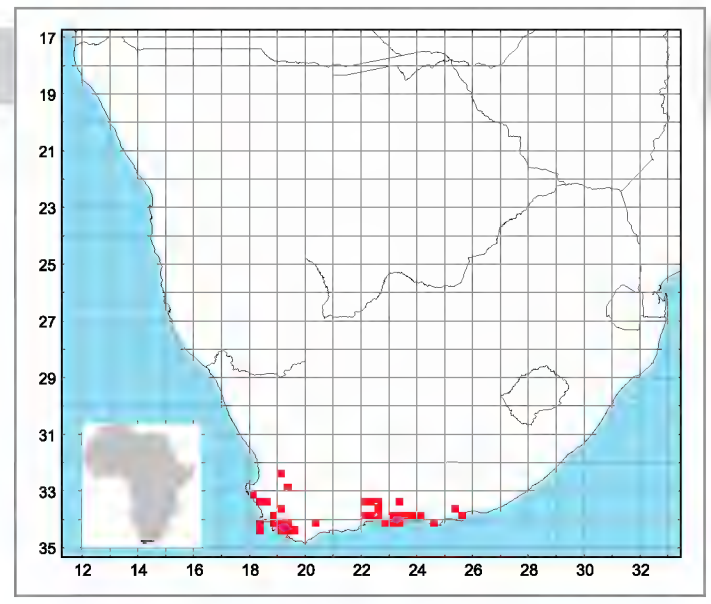
Onthophagus giraffa

(Hausmann, 1807)

= *Copris pectoralis* Thunberg, 1818
= *Copris platycera* Wiedemann, 1823

Global: LC (see IUCN Red List – LC)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: As *Copris giraffa*: 'Vorgebirges der guten Hoffnung' [Cape of Good Hope, South Africa]; *C. pectoralis*: 'majorem horum partem in capite bonae spei collegi' [amongst material mostly collected in the Cape of Good Hope, South Africa]; *C. platycera*: 'Prom. bon. sp.' [Cape of Good Hope].

Taxonomy: Accepted Group 17 species; sexually dimorphic (head), character varies in prominence with body size.

Distribution: Dry coastal lowlands and coastal mountains from SW Western Cape to Eastern Cape, South Africa, encompassing the moister SW of the winter rainfall region and the bimodal (spring/autumn) rainfall region; W/E disjunction would be a collection artefact.

Locality data (mean ± SD, range): Altitude: 480 ± 508, 0–1 993 m; annual rainfall: 408 ± 78, 246–564 mm; annual temperature (max. + min. /2): 15.8 ± 1.9, 9.4–18.0°C (N=52).

Habitat: Available quantitative data are difficult to interpret; averaged data suggest generalist habits; however, local data from natural West Coast shrubland at Pampoenvlei suggest bias to deep sand (74) compared to sandy loam (8); on deep sands of the Cape Peninsula, abundance is lower in dense natural *Restio*-dominated shrubland (519) than in Kikuyu grass pasture (1 041) created by clearance of natural shrubs; similar results are shown on deep sands of the West Coast at Geelbek (sparse grass = 669, open shrubland = 199); DBRU collection records from sand (8), sandy loam (5), sandy clay loam (4) in disturbed pasture (11), natural shrubland (3), open woodland (1), forest (1), fallow crop field (1).

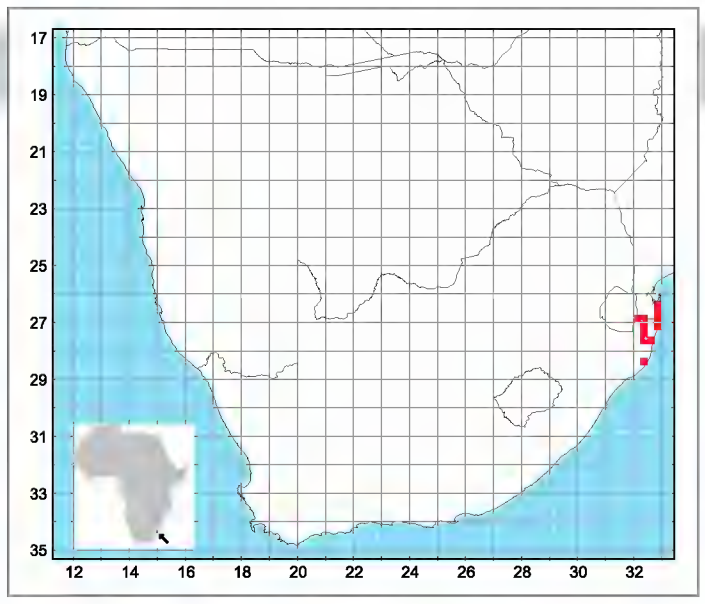
Food types: No quantitative assessment; DBRU collection records from dung of cattle (18) and single records from buffalo, elephant, horse, human/cattle dung mix.

Temporal activity: Diurnal flight activity during most of the year (Aug. to May); on Cape Peninsula and West Coast: peaks in spring (Aug. to Nov.) and autumn (Mar.) tailing off into dry mid-summer and cold mid-winter; peaks in both sclerotised and teneral adults in spring (Aug. to Nov.) and of teneral adults in late summer (Feb. to Mar.).

Bioregions South Africa: Most elements of Fynbos, Fynbos-Renosterveld and Renosterveld Bioregions (FO 1–3, 5–8), also West Strandveld (F 11) (Fynbos Biome).

Assessment rationale: EOO = 59 495 km²; widespread along SW and S coastline of South Africa, apparently with greater abundance in transformed pasture habitats than natural shrubland; although transformation for arable farming is extensive, particularly in the centre of its range, it is assessed as Least Concern (LC) since it remains well represented on various soil types in both natural and disturbed habitat used for grazing.

Conservation measures: Assessment of conservation status would benefit from more clearly defined data on soil, vegetation and dung type associations, particularly precise responses to widespread habitat transformation; protected in West Coast and Bontebok national parks, also Cape of Good Hope Nature Reserve.



Onthophagus giuseppecarpanetoi

Tagliaferri & Moretto, 2012

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Mozambique, [Maputo], Matutuine distr., Lake Piti (eastern shore), 26°36'40.9"S 32°53'19.7"E'.

Taxonomy: Accepted Group 7 species; sexually dimorphic (head, front tibiae); characters vary a little with body size.

Distribution: Open vegetation on deep coastal sands of the Maputaland Centre of Endemism: SE Mozambique and NE coastal KwaZulu-Natal, South Africa.

Locality data (mean ± SD, range): Altitude: 36 ± 47, 0–222 m; annual rainfall: 754 ± 78, 634–971 mm; annual temperature (max. + min. /2): 22.3 ± 0.3, 21.6–22.6°C (N=27).

Habitat: No quantitative assessment of soil association; on deep sand in Maputo Special Reserve: strong bias to grassland on fossil lagoons (30.0), few in sand forest patches (large, 1.1; medium, 1.9; small, 2.7) or cooler coastal dune forest (0.03); severely limited DBRU collection records in grassland (2), shaded thicket (1).

Food types: No quantitative assessment; known from elephant dung.

Temporal activity: Flight activity during darkness in the summer rainy season (Oct. to Jan.).

Ecoregions Mozambique: Maputaland Coastal Forest Mosaic (AT0119).

Bioregions South Africa: N Indian Ocean Coastal Belt Biome (CB) and adjoining SE Lowveld (SVl) Savanna Biome.

Assessment rationale: EOO = 8 945 km²; probably a deep sand specialist primarily in open vegetation, but no formal data to support soil association; known EOO relatively small, but most records from protected areas; therefore, currently assessed as Least Concern (LC).

Conservation measures: Assessment of conservation assessment would be improved by data to support soil specialisation and determine dung type associations; protected in Tembe Elephant Park and uMkhuze Game Reserve (South Africa), Maputo Special Reserve (Mozambique).

Onthophagus gonopygus

d'Orbigny, 1902

= *Onthophagus phalopsides* Frey, 1955

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. gonopygus*: 'Côte du Congo.....Benguella' [?Congo coast; Benguela, Angola]; *O. phalopsides*: 'Karibib, S. W. Afrika' [Karibib, Namibia].

Taxonomy: Accepted Group 30 species; recent synonymy of *O. phalopsides* with *O. gonopygus* based on material from Benguela; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.

Distribution: Arid edge of W escarpment in Namibia; presumably also arid coastal regions of SW Angola near type locality of Benguela; one record from Tswalu Kalahari Reserve (Northern Cape, South Africa) requires validation; citations from tropical Democratic Republic of the Congo (DRC), Gabon also require validation.

Locality data (mean ± SD, range): Altitude: 881 ± 443, 58–1 884 m; annual rainfall: 185 ± 104, 14–375 mm; annual temperature (max. + min. /2): 17.0 ± 1.4, 13.3–18.8°C (N=17).

Habitat: No quantitative assessment; DBRU collection records from sand (7), sandy loam (1) in grassland (2), scrub/shrubland (5), open woodland (1).

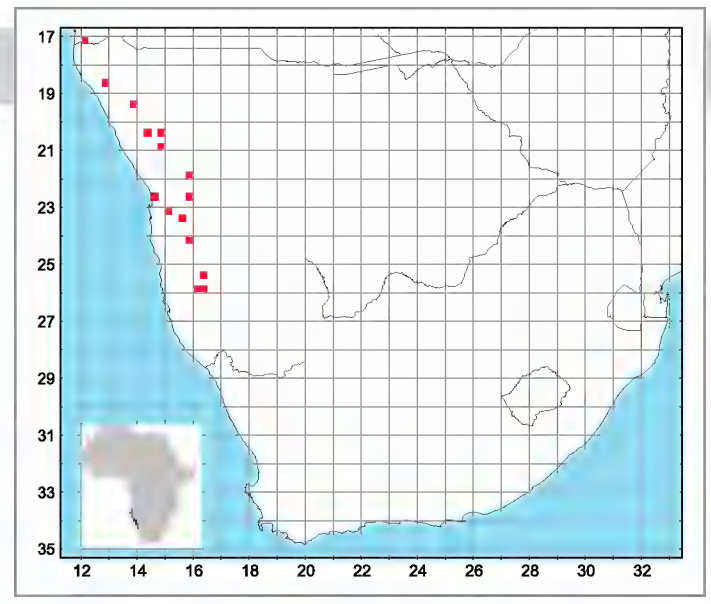
Food types: No quantitative assessment; DBRU collection records from dung of cattle (5), horse (2).

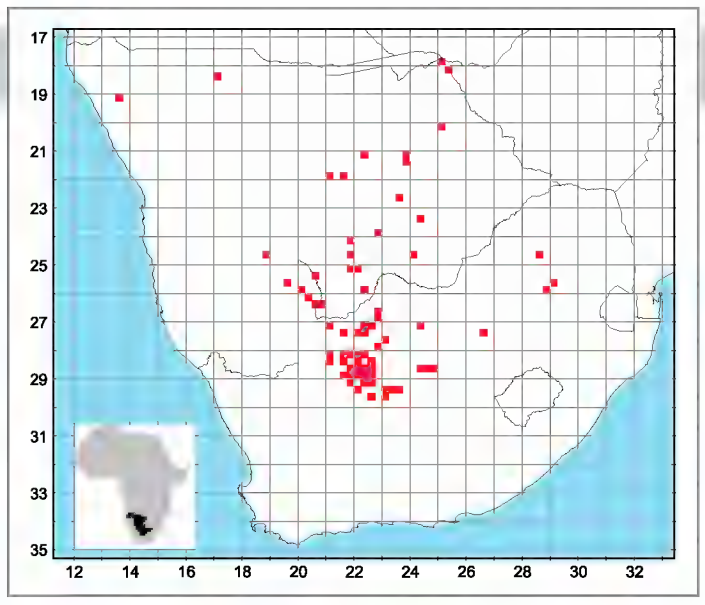
Temporal activity: Diel flight periodicity unknown; active in late summer rainy season (Feb. to Apr.).

Ecoregions Namibia: Namibian Savanna Woodlands (AT1316), Namib Desert (AT1315).

Assessment rationale: EOO = 102 535 km^2; wide range along the little-transformed, arid, SW coastal region that is used primarily for grazing of domestic livestock and conservation; AOO would be smaller if association with sandy soils is supported by quantitative data; nevertheless, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by a survey to ascertain the full EOO and quantitative data on ecological associations; protected in parts of Namib-Naukluft National Park (Namibia).





Onthophagus granulifer

Harold, 1886

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Oranje-Freistaat' [Free State, South Africa].

Taxonomy: Accepted Group 24 species; sexually dimorphic (head), characters vary in prominence with body size.

Distribution: Deep sands of S Kalahari: South Africa, Botswana, Namibia, Angola; tentative identification of species recorded at three E outlier localities; validation required for citations from Zimbabwe, Democratic Republic of the Congo (DRC) owing to presence of close relatives.

Locality data (mean ± SD, range): Altitude: 1 060 ± 115, 799–1 345 m; annual rainfall: 299 ± 117, 171–813 mm; annual temperature (max. + min. /2): 19.7 ± 1.1, 16.8–23.1°C (N=127).

Habitat: No adequate quantitative assessment; in Northern Cape: high frequency in SW Kalahari (92.8%, 90/97 samples) and high abundance on deep sand (33.5/sample) or sandy loam (21.5); DBRU collection records exclusively on deep sand (15) in grassland (5), scrub/shrubland (5), open woodland (4).

Food types: In Botswana: well represented on various dung types, but with clear bias: pig (4 052), sheep (2 179), elephant (1 363), cattle (550), poorly attracted to carrion: chicken livers (34) (cited as *Onthophagus* sp. k); DBRU collection records on dung of cattle (10), wildebeest (1), elephant (2), donkey (1).

Temporal activity: Flight activity in darkness primarily during the summer rainy season (Oct. to May).

Ecoregions Namibia, Botswana: N Namibian Savanna Woodlands (AT1316), Kalahari Xeric Savanna (AT1309), Angolan Mopane Woodlands (AT0702), Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian and Mopane Woodlands (AT0725), Zambezian Baikiaea Woodlands (AT0726).

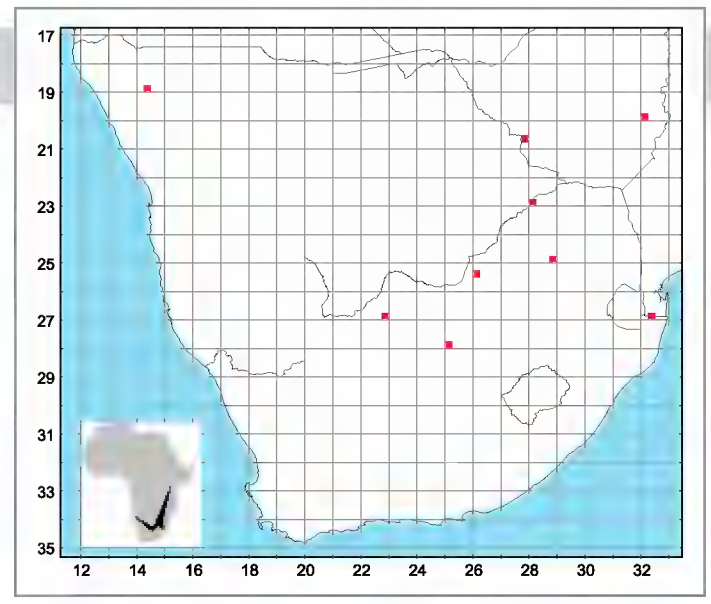
Bioregions South Africa: Kalahari Duneveld (SVkd), Eastern Kalahari Bushveld (SVk) (Savanna Biome); sand patches in N Bushmanland (NKb), N Upper Karoo (NKu) (Nama Karoo Biome); sand outliers in Dry Highveld Grassland (Gh) (Grassland Biome), Central Bushveld (SVcb) (Savanna Biome).

Assessment rationale: EOO = 1 080 205 km^2 (possibly underestimated); AOO would be limited by soil specialisation although deep sand is widespread across the EOO; SW part of large range is centred on a little-transformed region used primarily for conservation and grazing of farm livestock to which it is attracted in abundance; assessed as Least Concern (LC).

Conservation measures: Asessment of conservation status would be improved by better quantitative data on habitat associations; protected in Kgalagadi Transfrontier Park (South Africa/Botswana).

Onthophagus graphicus

Wallengren, 1881



No synonyms

Global: DD

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'ad Christianam inventum' [interpreted as Christiana, South Africa].

Taxonomy: Accepted Group 15 species; another group member, *Onthophagus maculatus* (Fabricius, 1801), is now assigned to the genus *Paracatonomus* Paulian, 1932; however, pending validation of changed generic affiliations of *O. graphicus*, we continue to treat it as an *Onthophagus* species.

Distribution: Widespread distribution in dry savanna from S to E Africa; patchiness possibly a collection artefact due to food specialisation: South Africa, Zimbabwe, Botswana, Namibia, Kenya.

Locality data (mean ± SD, range): Altitude: 935 ± 373, 58–1 201 m; annual rainfall: 486 ± 157, 279–717 mm; annual temperature (max. + min. /2): 20.0 ± 1.7, 17.8–22.6°C (N=9).

Habitat: Not known.

Food types: No quantitative assessment; two records from meat bait; recorded to dead millipede bait in Kenya (Krell 2004).

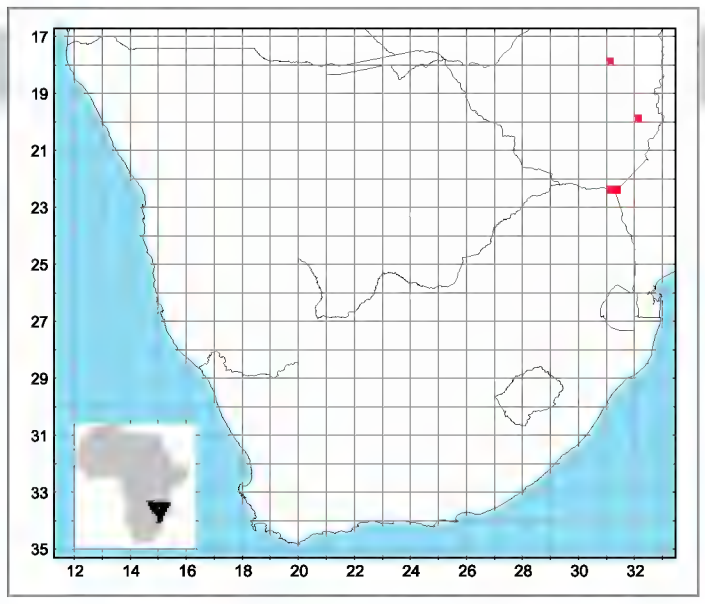
Temporal activity: Diel flight periodicity unknown; recorded in the summer rainy season (Nov. to Feb.).

Ecoregions Namibia, Zimbabwe: N Namibian Savanna Woodlands (AT1316), Southern African Bushveld (AT0717), Zambezian and Mopane Woodlands (AT0725).

Bioregions South Africa: Eastern Kalahari Bushveld (SVk), Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 1 088 955 km^2 (gross estimate); scattered records may be a collection artefact related to putative carrion specialisation, but further supporting data are required; probably deserves Least Concern (LC) status on basis of widespread range, but currently assessed as Data Deficient (DD) since poorly known taxonomically and ecologically.

Conservation measures: A quantitative survey of ecological associations is required before an assessment may be made of conservation status; protected within Stevensford (Botswana) and Ndumo (South Africa) game reserves.



Onthophagus herus

Péringuey, 1901

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Southern Rhodesia (Salisbury)' [Harare, Zimbabwe].
Taxonomy: Accepted Group 16 species; sexually dimorphic (head, fore tibia, prothoracic disc), characters vary in prominence with body size.
Distribution: Dry to moist shaded vegetation on the Mozambique Coastal Plain and upland moist savanna in SE Africa; NE tip South Africa, Zimbabwe, Mozambique; also cited from Malawi, Tanzania, Democratic Republic of the Congo (DRC).
Locality data (mean ± SD, range): Altitude: 439 ± 489, 76–1 410 m; annual rainfall: 722 ± 237, 383–1 007 mm; annual temperature (max. + min. /2): 23.3 ± 2.6, 18.7–25.9°C (N=8).
Habitat: No quantitative assessment; several Ditsong Museum records from dense woodland or forest.
Food types: No quantitative assessment; single male type found in carrion; single DBRU collection record from baboon dung.
Temporal activity: Diel flight periodicity unknown, but presumably diurnal during the summer rainy season (Nov. to Mar.).
Ecoregions Zimbabwe: Dense riverine vegetation at edges of Zambezian and Mopane Woodlands (AT0725) and Southern Miombo Woodland (AT0719).
Bioregions South Africa: Mopane (SVmp) (Savanna Biome).
Assessment rationale: EOO = 1 168 730 km^2 (gross estimate); AOO would be very much smaller owing to probable vegetation (shade) and food type specialisation (omnivore dung, carrion), but this needs quantitative support; if correct, clearance of dense woody vegetation would be detrimental to population density; however, S extremity of range in NE South Africa entirely protected; currently assessed as Least Concern (LC) on basis of wide distribution.
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; protected in Kruger National Park (South Africa).

Onthophagus hyaena

(Fabricius, 1801)

= *Onthophagus impictus* Fahraeus, 1857
= *Onthophagus scabrosus* Péringuey, 1901

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Scarabaeus hyaena*: 'Cap. Bon. Spei.' [Cape of Good Hope, South Africa]; *O. impictus*: 'in terra Natalensi' [KwaZulu-Natal, South Africa]; *O. scabrosus*: 'Natal (Newcastle, Frere), Transvaal (Potchefstroom, Lydenburg)' [South Africa: KwaZulu-Natal; Potchefstroom, North-West Province; Mashishing, Mpumalanga].

Taxonomy: Accepted Group 9 species, but requires validation; type should be compared with that of putative closely related, *O. cineraceus* d'Orbigny, 1902 (type locality: Cape Town); synonymy of *O. impictus* and *O. scabrosus* are probable errors as type localities fall outside of ranges of *O. cineraceus* and *O. hyaena*; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.

Distribution: Lowland, S coastal belt, Eastern Cape and highlands along W Lesotho border primarily in E Free State, South Africa; disjunction may be a collection artefact, but probably real across unsuitable bioregions.

Locality data (mean ± SD, range): Altitude: 1 250 ± 869, 21–2 199 m; annual rainfall: 614 ± 116, 421–814 mm; annual temperature (max. + min. /2): 15.2 ± 1.7, 11.2–17.6°C (N=38).

Habitat: No quantitative assessment; DBRU collection records on sand (3), sandy loam (14), sandy clay loam (11) in pasture/grassland (25), fallow crop fields (2); also recorded in fynbos shrubland and forest.

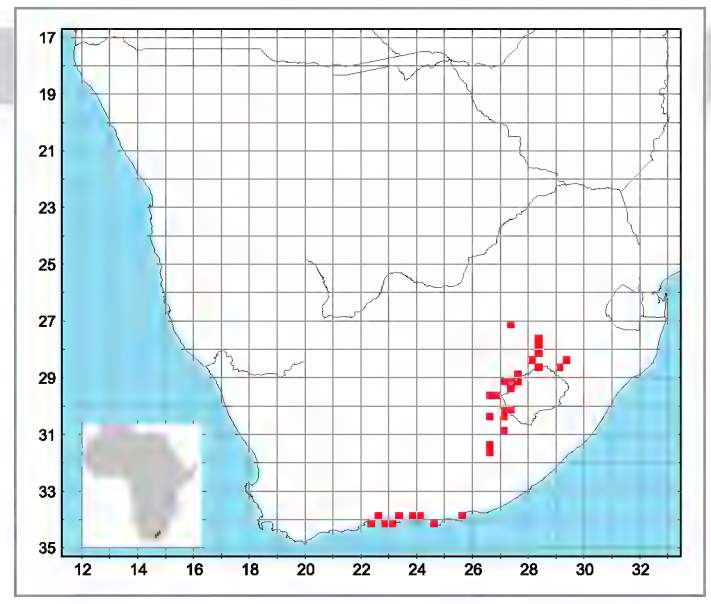
Food types: No quantitative assessment; DBRU collection records from dung of cattle (30), horse (2), human/cattle mix (2).

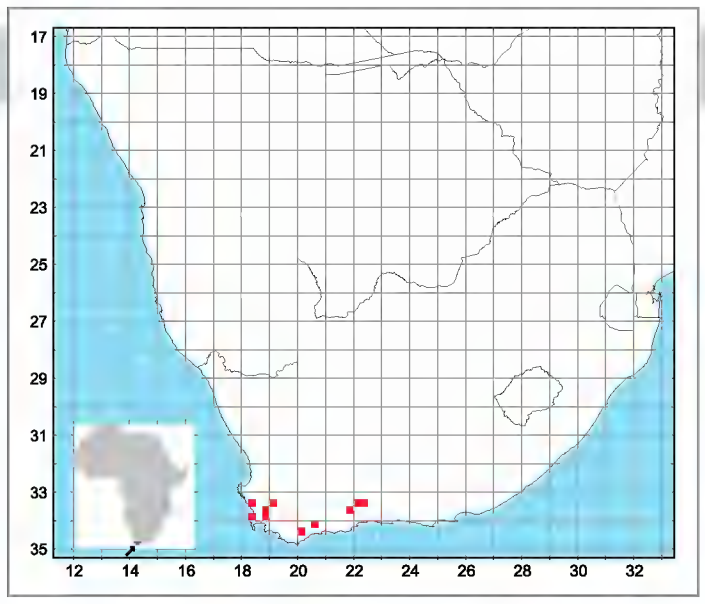
Temporal activity: Diel flight periodicity unknown, but probably diurnal, primarily in the summer rainy season (Oct.–May) or autumn in bimodal rainfall region of S coast (Feb.–May).

Bioregions South Africa: S Mesic Highveld Grassland (Gm), SE tip Dry Highveld Grassland (Gh), S tip Drakensberg Grassland (Gd) (Grassland Biome); Eastern Fynbos-Renosterveld (FO 6) (Fynbos Biome).

Assessment rationale: EOO = 38 760 km^2; vegetation associations unclear; primarily recorded in pasture grassland, but also series from Tsitsikamma Forest; however, considering fairly large range and frequent occurrence in farmland pastures, including fallow crop fields, currently assessed as LC.

Conservation measures: Taxonomic issues need to be resolved by comparison of types of *O. hyaena* and *O. cineraceus* plus possible revision of the status and relationships of *O. impictus* and *O. scabrosus*; assessment of conservation status of *O. hyaena* would be improved by quantitative data on ecological associations; protected in Tsitsikamma forest.





Onthophagus immundus

Boheman, 1858

= *Onthophagus vitulus* Péringuey, 1901

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. immundus*: 'Promontorium Bonae Spei' [Cape of Good Hope, South Africa]; *O. vitulus*: 'Cape Colony (Cape Town, Stellenbosch, Worcester, Paarl, Malmesbury)' [Western Cape, South Africa].

Taxonomy: Accepted Group 31 species (subgenus: *Furconthophagus*); sexually dimorphic (head), characters vary somewhat in prominence with body size.

Distribution: Centred on Renosterveld regions, SW Western Cape to W Eastern Cape, South Africa.

Locality data (mean ± SD, range): Altitude: 521 ± 367, 62–962 m; annual rainfall: 340 ± 86, 246–539 mm; annual temperature (max. + min. /2): 16.0 ± 1.4, 13.1–18.2°C (N=13).

Habitat: In Western Cape: not recorded on cooler Cape Peninsula (0), rare on warmer W coastal sands (1), primarily recorded on sandy loam in three pastures cleared of natural shrubland in Darling Hills (70, 74, 23); DBRU collection records from sand (2), sandy loam (7), sandy clay loam (1) in pasture/grassland (7), or crop fields (4).

Food types: No quantitative assessment; DBRU collection records entirely from cattle dung (11).

Temporal activity: Diel flight periodicity unknown; recorded in all months of the year except mid-winter (Aug. to May); but, in Western Cape: primarily recorded in spring (sclerotised: Aug. to Oct., especially Aug.; tenerals: especially Oct.), rare in autumn (May).

Bioregions South Africa: Centred on West Coast Renosterveld (FO 7), East Coast Renosterveld (FO 8), Western Fynbos-Renosterveld (FO 5) (Fynbos Biome).

Assessment rationale: EOO = 26 615 km^2; restricted to SW South Africa; occupies a fair-sized EOO although AOO would, presumably, be smaller according to occurrence of Renosterveld; although endemic to the winter and W bimodal rainfall regions, all known vegetation records are from pasture or crop fields cleared of natural shrubland; because of large EOO and apparent tolerance of habitat disturbance, currently assessed as Least Concern (LC), although monitoring of population density would be advisable, particularly in the most highly disturbed W part of its range.

Conservation measures: Assessment of conservation status would be improved by further quantitative data on ecological associations, particularly formal comparisons of population density in natural versus replacement pasture vegetation since most Renosterveld has been transformed; protected in the Eastern Cape in the conservation area incorporating Swartberg Pass.

Onthophagus interstitialis

Fahraeus, 1857

= *Onthophagus glaber* Boheman, 1857

Global: LC
Endemic: RSA, Eswatini

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. interstitialis*: 'in terra Natalensi' [KwaZulu-Natal, South Africa]; *O. glaber*: 'Caffraria interiore' [probably interior of South Africa].

Taxonomy: Accepted Group 7 species probably belonging to the new subgenus, *Bicornonthophagus* Tagliaferri & Moretto, 2012; sexually dimorphic (head, prothoracic disc), characters vary somewhat in prominence with body size.

Distribution: Widespread across drier W Highveld to moist NE Highveld and NE lowlands, South Africa; record from Zimbabwe requires validation; currently considered primarily endemic to South Africa.

Locality data (mean ± SD, range): Altitude: 1 042 ± 562, 43–1 914 m; annual rainfall: 653 ± 119, 435–947 mm; annual temperature (max. + min. /2): 17.9 ± 3.0, 12.9–23.6°C (N=95).

Habitat: In Gauteng bushveld: extreme bias to sandy clay loam (56) compared to deep sand (2) and to grassland (47) compared to open woodland (4) and shaded thickets (7); in lowlands of uMkhuze Game Reserve: sand (2.3), duplex soil (sand over clay) (55.8), sandy clay loam (238.8), clay (18.0) with 64% of abundance in grassland; supported by DBRU collection records primarily from NE lowlands: clay (9), sandy clay loam (23), sandy loam (18), sand (8) in grassland/pasture (28), open shrub/woodland (11), forest/thicket (3); as well as fallow crop fields (4).

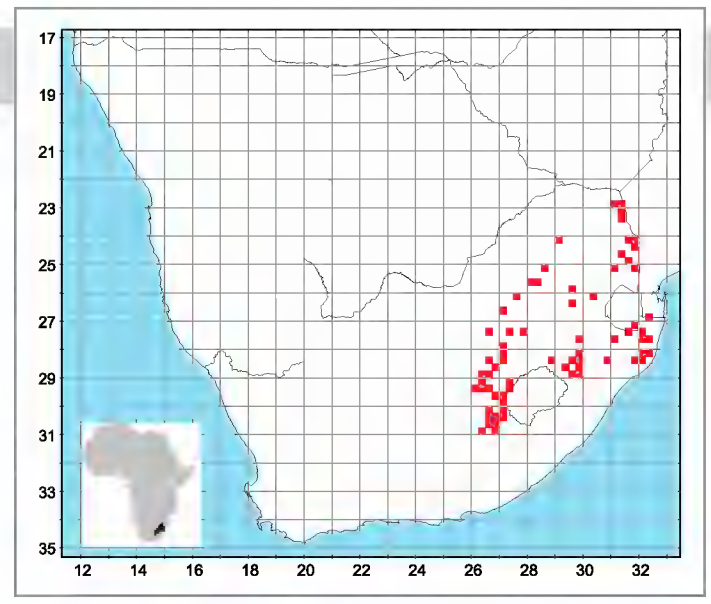
Food types: In Ithala Game Reserve: extreme bias to dung of pig (119) compared to horse (1) and cattle (2); however, DBRU collection records biased to more frequently recorded dung of cattle (54), wildebeest (1), elephant (8), rhinoceros (2), zebra (3), horse (1), warthog (1), human/cattle mix (3).

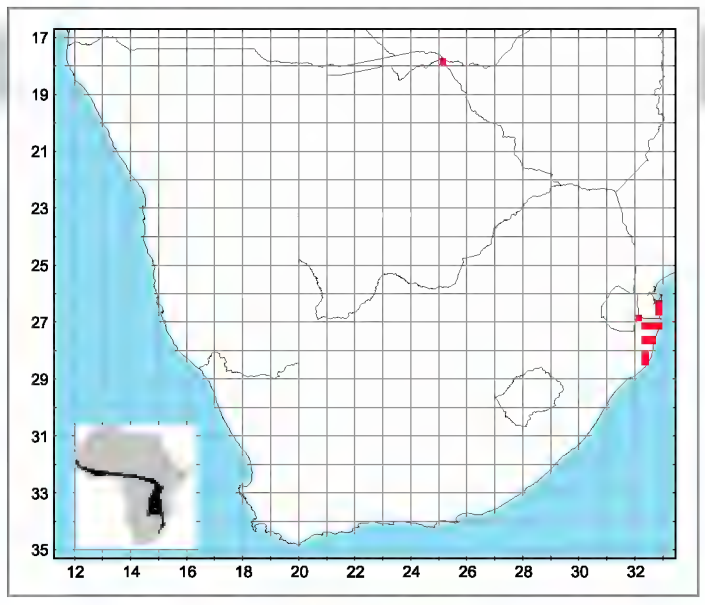
Temporal activity: Flight activity in darkness primarily during the summer rainy season (Oct. to May); in Gauteng bushveld primarily active Oct. to Feb., tailing off thereafter; attracted to light.

Bioregions South Africa: Moister E Dry Highveld Grassland (Gh), warmer N Sub-Escarpment Grassland (Gs) (Grassland Biome); Lowveld (SVl), Mopane (SVmp) (Savanna Biome); scattered records in warmer parts of Mesic Highveld Grassland (Gm).

Assessment rationale: EOO = 251 810 km^2; AOO presumably smaller due to specialisation on finer-grained soils; high frequency of records from cattle dung across farmland despite measured bias to omnivore dung, which might, however, lower population density; assessed as Least Concern (LC) on basis of widespread occurrence.

Conservation measures: Assessment of conservation would be improved by tests of population density in improved pasture versus natural highveld grasslands; lowland populations protected in Kruger National Park, uMkhuze and Hluhluwe–iMfolozi game reserves.





Onthophagus juvencus

Klug, 1835

No synonyms

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Isle de Prince' [Isle of Príncipe, São Tomé e Príncipe, Gulf of Guinea].

Taxonomy: Accepted Group 12 species (subgenus: *Trichonthophagus*), but, given the type locality and extremely wide cited distribution, S, E, and W African representatives should, perhaps, be re-examined for validity as a single species; minor sexual dimorphism (head).

Distribution: Widespread from S to E to W Africa: South Africa, Mozambique, Botswana, Namibia, Kenya, Príncipe Island, Côte d'Ivoire; also cited from Ethiopia, Eritrea, Uganda, Rwanda, Democratic Republic of the Congo (DRC), Gabon, Chad, Niger, Benin, Guinea (Conakry), Guine (Bissau), Gambia, Senegal; in southern Africa: open vegetation on deep sands of the E coast and Okavango Delta.

Locality data (mean ± SD, range): Altitude: 67 ± 185, 0–919 m; annual rainfall: 865 ± 173, 646–1 275 mm; annual temperature (max. + min. /2): 22.5 ± 0.9, 21.6–24.8°C (N=25).

Habitat: On deep sand in Maputo Special Reserve: almost exclusively in grassland of fossil lagoons (7.43) compared to sand forest patches (large, 0; medium, 0; small, 0.02); DBRU collection records from sand (7), sandy clay loam (1) in grassland (13), shrubland (1), open woodland (1).

Food types: No quantitative assessment; DBRU collection records from dung of cattle (5), human (1), human/buffalo mix (1).

Temporal activity: Flight activity during darkness (18:00–22:00); recorded both during the summer rainy season (Oct. to Apr.) and mild dry season at the coast (May, July, Aug.).

Ecoregions Botswana, Mozambique: Zambezian and Mopane Woodlands (AT0725) in Okavango; Maputaland Coastal Forest Mosaic (AT0119), also Southern Zanzibar-Inhambane Coastal Forest Mosaic (AT0128), Zambezian Coastal Flooded Savanna (AT0906) (not shown on map).

Bioregions South Africa: Primarily Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 2 971 515 km^2 (underestimated, gross estimate); cited from localities across a very wide range, but in southern Africa primarily range restricted to moist grasslands on deep E coastal sands; also recorded as a rarity in Okavango Swamps and an untraced locality in Namibia ('Okurokandovi sandveld'); assessed as Least Concern (LC) owing to wide range and frequent occurrence in open vegetation and protected areas in South Africa.

Conservation measures: Assessment of conservation status would be improved by quantitative data on soil and food type associations in S, E and W Africa; in southern Africa, protected in iSimangaliso Wetland Park (World Heritage Site) (South Africa), Maputo Special Reserve (Mozambique).

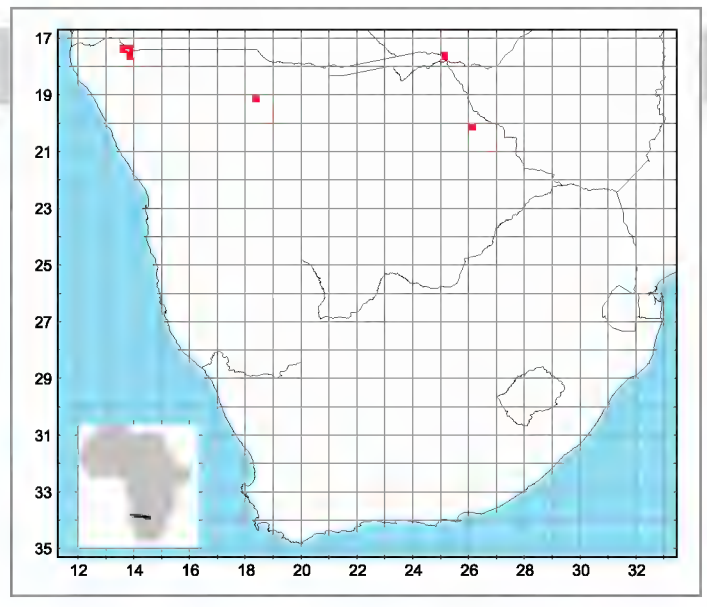
Onthophagus kochi

Frey, 1957

No synonyms

Global: DD
Endemic: Botswana, Namibia

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: 'Tulli Distr., Betschuanaland/Südafrika' (inexact locality: Tuli Block, NE Botswana).

Taxonomy: Accepted Group 19 species; sexually dimorphic (head), characters vary in prominence with body size; identity of species treated, here, as *O. kochi*, requires validation in comparison with *O. otjivarongus* Balthasar, 1967, described from Abachaus (N Namibia); differs from close relative in Zambezian and Mopane Woodlands (AT0725) of the Kruger National Park (South Africa).

Distribution: Dry savanna: N Namibia, N Botswana.

Locality data (mean ± SD, range): Altitude: 949 ± 222, 683–1 246 m; annual rainfall: 442 ± 105, 356–660 mm; annual temperature (max. + min. /2): 20.4 ± 1.9, 17.8–22.7°C (N=7).

Habitat: No quantitative assessment; no records.

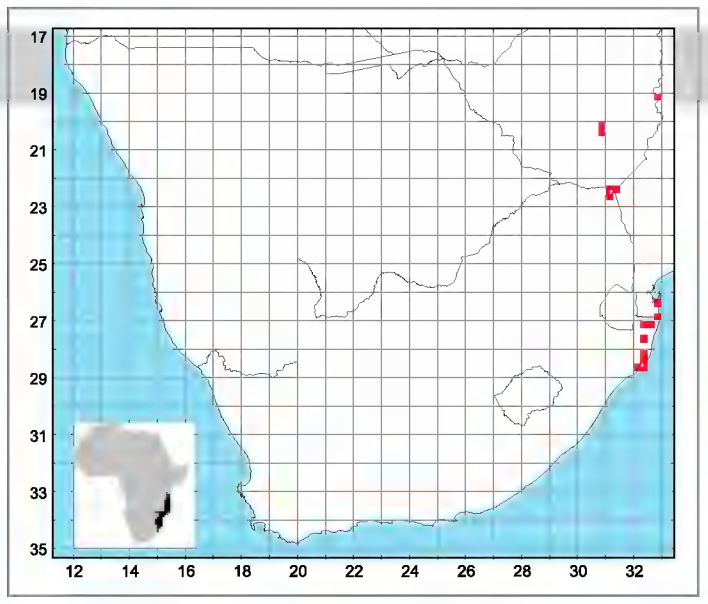
Food types: No quantitative assessment; reference material recorded from baits of human dung and meat; a few from banana.

Temporal activity: Diel flight periodicity unknown, but probably in darkness like other Group 19 species; recorded primarily in the summer rainy season (Oct. to Mar.).

Ecoregions Namibia, Botswana: Namibian Savanna Woodlands (AT1316), Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian and Mopane Woodlands (AT0725).

Assessment rationale: EOO = 224 650 km^2; recorded from scattered localities across a wide area of dry savanna, but poorly known ecologically although Group 19 species are considered to comprise carrion specialists; currently assessed as Data Deficient (DD), but probably Least Concern (LC).

Conservation measures: Before conservation status may be adequately assessed, this species requires validation as *O. kochi*; quantitative data on ecological associations are also required; not currently known from any protected region.



Onthophagus lacustris

Harold, 1877b

No synonyms

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Nyassa' [Lake Malawi region].

Taxonomy: Accepted Group 7 species; aedeagi of NE Tanzanian and South African specimens identical, but minor differences in punctation.

Distribution: Moister, densely vegetated parts of tropical and subtropical E seaboard; in the S: Mozambique Coastal Plain and moist edges of major river valleys (Limpopo, Save, Zambezi); Tanzania, Mozambique, Malawi, Zimbabwe, South Africa; also reported from Kenya; record from Democratic Republic of the Congo (DRC) requires validation (probable error).

Locality data (mean ± SD, range): Altitude: 245 ± 404, 0–1 464 m; annual rainfall: 846 ± 215, 383–1 659 mm; annual temperature (max. + min. /2): 22.3 ± 1.5, 17.2–25.2°C (N=38).

Habitat: In uMkhuze Game Reserve: recorded only on deep sand (3.3) and in shaded habitat, not on sandy clay loam or clay (0.0); on deep sand in Maputo Special Reserve: recorded only in sand forest (large patches: 16.4, medium: 19.6, small: 7.2) and cooler coastal dune forest (6.6), not in grassland (0); supported by limited DBRU collection records from sand (2) in forest (8) or tree plantation (2); recorded on finer-grained soil types elsewhere, e.g. Tanzania (East Usambaras).

Food types: No quantitative assessment; limited DBRU collection records from human/cattle or buffalo dung mix (5); also dung of baboon (1), cattle (2).

Temporal activity: Flight activity in darkness, primarily during the summer rainy season (Oct. to Mar.); attracted to light.

Ecoregions Zimbabwe, Mozambique: Southern Miombo Woodland (AT0719), Maputaland Coastal Forest Mosaic (AT0119).

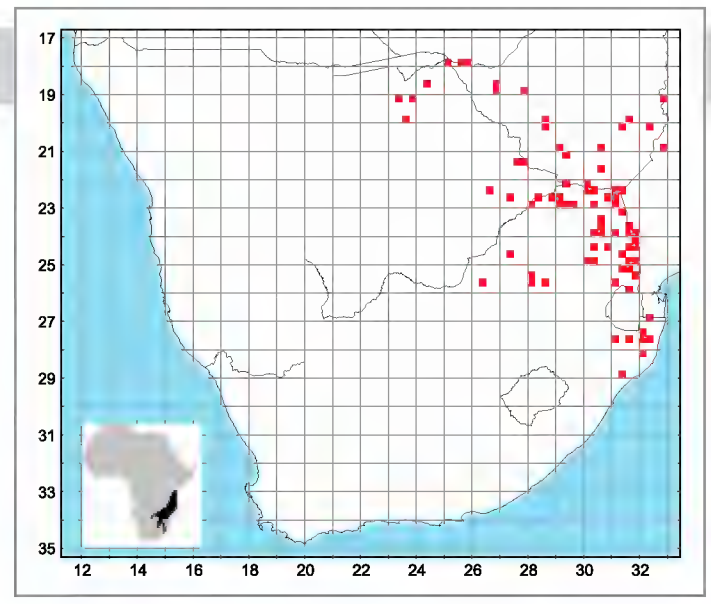
Bioregions South Africa: N part of Indian Ocean Coastal Belt Biome (CB); densely vegetated areas in Mopane (SVl) (Savanna Biome).

Assessment rationale: EOO = 874 260 km^2 (gross estimate, validated range); AOO would be smaller owing to shade specialisation in forest or dense woodland; soil association data may be characteristic only of coastal NE South Africa; possible bias to omnivore dung, but not well supported; clearance of dense shady vegetation would be detrimental but assessed as Least Concern (LC) owing to widespread range and protection in various reserves.

Conservation measures: Assessment of conservation status would be improved by quantitative data on soil and vegetation associations at different points across the EOO; protected in uMkhuze Game Reserve, Kruger National Park (South Africa), Lake Mutirikwe Game Reserve (Zimbabwe), Gorongosa National Park (Mozambique).

Onthophagus lamelliger

Gerstaecker, 1871



No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Zanzibar' [Tanzania].

Taxonomy: Accepted Group 31 species (subgenus *Furconthophagus*); sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.

Distribution: Centred on finer-grained soils in moist, lower-altitude savanna from southern to southern central Africa; EOO in tropics needs to be validated by comparison with close relatives, *O. exisiciceps* d'Orbigny (E to W central Africa) and *O. ochropygus* d'Orbigny (W central Africa); South Africa, Botswana, Zimbabwe, Mozambique, Malawi, Tanzania; records from Angola, Zambia, Kenya require validation.

Locality data (mean ± SD, range): Altitude: 591 ± 353, 55–1 573 m; annual rainfall: 593 ± 170, 304–1 177 mm; annual temperature (max. + min. /2): 21.7 ± 1.7, 15.1–25.2°C (N=107).

Habitat: In uMkhuze Game Reserve: conflicting results, deep sand (186.8), sand on clay (1 180.4), sandy clay loam (354.6), clay (1 155.6) with a 68% bias to shade; DBRU collection records weakly biased to finer-grained soils, sand (12), sandy loam (13), sandy clay loam (10), clay (2), and strongly biased to more shaded vegetation, grassland/pasture (3), shrubland (6), open woodland/woodland (23), forest/thickets (6); fallow crop field (1).

Food types: At Phalaborwa: strong bias to dung of omnivores (pig, 21 850) compared to monogastric (elephant, 6 335) or ruminant herbivores (cattle, 4 125); DBRU collection records from various dung types, buffalo (1), cattle (24), wildebeest (2), impala (1), donkey (2), horse (2), zebra (2), elephant (5), rhinoceros (2), warthog (1), human (2), human/cattle mix (3).

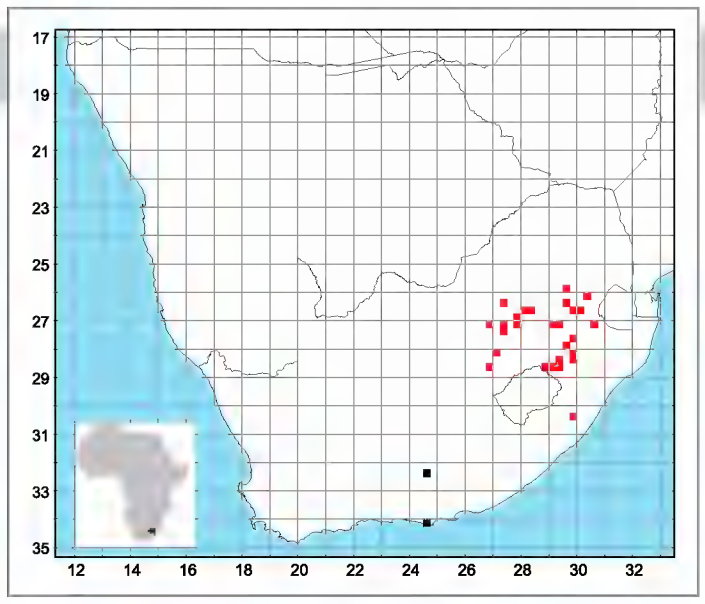
Temporal activity: Flight activity in darkness, primarily during the summer rainy season (Oct. to Apr.); at Phalaborwa: much more abundant in warm conditions after light rainfall (18 612) than under dry conditions (8 544) or after heavy rainfall (5 146).

Ecoregions Botswana, Zimbabwe: Primarily Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian and Mopane Woodlands (AT0725), Southern African Bushveld (AT0717).

Bioregions South Africa: Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome); marginal in two other bioregions.

Assessment rationale: EOO = 1 440 975 km^2; abundant and widespread; more or less equally abundant in conserved and disturbed areas of a mining concession at Phalaborwa; perceived bias to finer-grained soils not well supported by available data; clearance of woodland would, presumably, influence population density owing to bias to partially shaded vegetation; assessed as Least Concern (LC) owing to extensive EOO and great local abundance on various dung types in both reserves and exploited areas.

Conservation measures: Assessment of conservation status would be improved by further data on soil associations; in South Africa protected in various reserves, especially, uMkhuze Game Reserve and Kruger National Park.



Onthophagus lamnifer

d'Orbigny, 1902

No synonyms

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Transvaal' [N South Africa].
Taxonomy: Accepted Group 31 species (subgenus *Furconthophagus*); sexually dimorphic (head); characters vary greatly in prominence with body size.
Distribution: Apparently centred on moist upland grassland: South Africa; black squares (tentative localities) within range of close relative, *O. fritschi* d'Orbigny, 1902.
Locality data (mean ± SD, range): Altitude: 1 429 ± 344, 21–1 922 m; annual rainfall: 691 ± 105, 289–804 mm; annual temperature (max. + min. /2): 15.9 ± 1.3, 12.7–18.6°C (N=38).
Habitat: No adequate quantitative data; on sandy loam in Abe Bailey Nature Reserve (26°S; 1 496–1 541 m): strong bias to grassland (107.1 per sample) compared to open woodland (7.9); on sandy loam at more southerly farm Boschberg (28°S): almost exclusively recorded in mid-altitude grassland (1 264–1 303 m; 31) compared to Highveld Grassland (1 676–1 687 m; 1); DBRU collection records from sand (1), sandy loam (8), sandy clay loam (8), clay (2) with all validated records from grassland/pasture (16) bar for one record from a fallow crop field.
Food types: No quantitative data; DBRU collection records entirely from cattle dung (22).
Temporal activity: Diel flight periodicity unknown, but presumably diurnal during the summer rainy season (Oct. to May).
Bioregions South Africa: Validated range centred on E Dry Highveld Grassland (Gh), Mesic Highveld Grassland (Gm), NW Sub-Escarpment Grassland (Gs) (Grassland Biome).
Assessment rationale: EOO = 96 245 km² (validated range, red squares); limited data suggest a soil generalist with a bias to open grassland that is readily attracted to the dung of farm livestock although further quantitative data is required in support; also one record from a fallow crop field, which would suggest some tolerance of transformation across its validated range (25–69%, lower-altitude Gm); therefore, assessed as Least Concern (LC).
Conservation measures: Assessment of conservation status would be improved by further quantitative data on ecological associations; also data on altitudinal centring and a more exact measurement of EOO as regards W edge of range, which abuts onto that of very closely related *O. fritschi* d'Orbigny, 1902; protected in Abe Bailey Nature Reserve.

Onthophagus leroyi

d'Orbigny, 1902

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'Sud de l'Afrique orientale anglaise: Escarpment....Mombasa....Nord de l'Afrique orientale allemande: Kilima Ndjaro' [S Kenya: Escarpment, Mombasa; N Tanzania: Kilimanjaro].

Taxonomy: Accepted Group 23 species, but validation required for occurrence in the S although aedeagi of S and E African individuals appear the same or very similar; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.

Distribution: Wide climatic range in savanna with putative occurrence from lowlands in the S to lowlands and highlands in the N: NE South Africa, N Tanzania, S Kenya.

Locality data (mean ± SD, range): Altitude: 382 ± 296, 55–1 205 m; annual rainfall: 612 ± 152, 305–900 mm; annual temperature (max. + min. /2): 21.8 ± 1.3, 17.6–24.4°C (N=27).

Habitat: No quantitative assessment; DBRU collection records on sand (1), sandy loam (3), sandy clay loam (1) with bias to woody vegetation: shrubland (1), woodland (2), shaded forest/thicket (3).

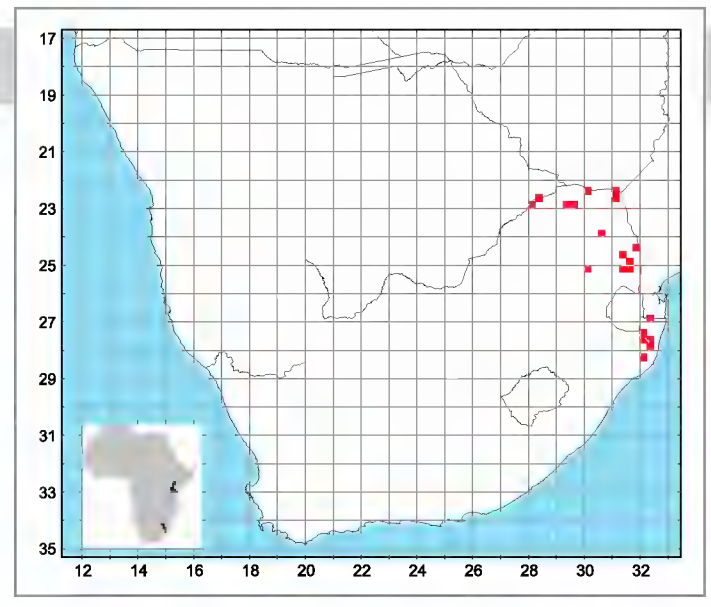
Food types: No quantitative assessment; DBRU collection records on dung of cattle (1), wildebeest (1), impala (1), elephant (2).

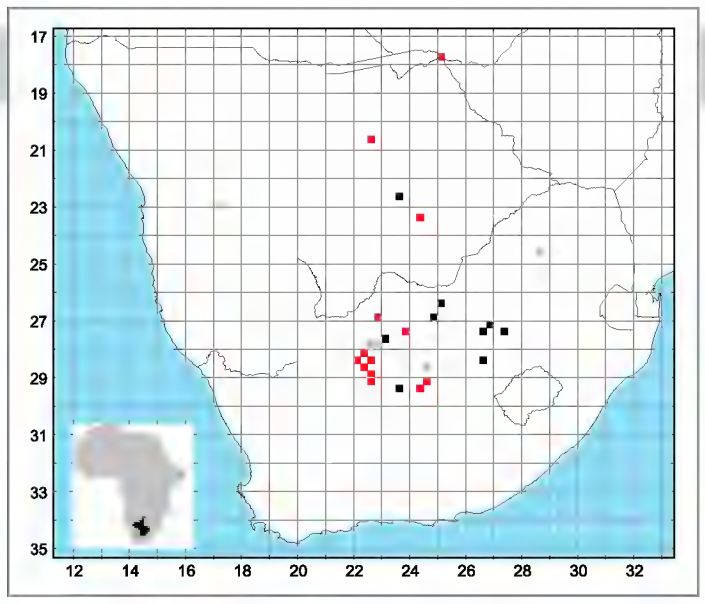
Temporal activity: Diel flight periodicity unknown, but probably in darkness like its close relative, *O. fimetarius* Roth, 1851; active during the summer rainy season (Oct. to Mar.).

Bioregions South Africa: Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 228 595 km^2 (putative estimate assumes disjunct populations); assuming S and E African populations are the same species, widespread in savanna, but ecologically poorly known; possible bias to woody vegetation could indicate potential threats from clearance in the S; however, often locally abundant with most available South African records from reserves; assessed as Least Concern (LC).

Conservation measures: Confirmation of single species status is required for E and S African populations; assessment of conservation status would be improved by quantitative ecological data, particularly vegetation associations and effects of woodland clearance on population density in the S; in South Africa, protected in Kruger National Park.





Onthophagus leucopygus

Harold, 1867

= *Onthophagus opimus* Péringuey, 1901

Global: LC (see IUCN Red List – LC as *O. impressicollis* Boheman, 1860)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. leucopygus*: 'Inneres Südafrika' [interior, South Africa]; *O. opimus*: 'Cape Colony' (Griqualand West) [South Africa].

Taxonomy: Accepted Group 24 species with varieties that are entirely metallic green or with elytra that are pale coloured; sexually dimorphic (head), characters vary in prominence with body size.

Distribution: Centred on deep Kalahari sands and its outliers: validated for South Africa, Botswana, Namibia; green variety (red squares), pale elytra variety (black squares), both varieties (grey squares).

Locality data (mean ± SD, range): Both varieties: Altitude: 1 224 ± 236, 817–1 998 m; annual rainfall: 381 ± 115, 254–660 mm; annual temperature (max. + min. /2): 18.8 ± 1.5, 15.9–22.7°C (N=35).

Habitat: No adequate quantitative assessment; in Northern Cape: recorded in very low numbers only on deep sands of the SW Kalahari (13.3% of samples, 13 of 98); DBRU collection records from sand (7), sandy loam (3), sandy clay loam (3) in grassland/pasture (5), shrubland (2), open woodland (4).

Food types: No adequate quantitative assessment; on deep sands in Botswana: recorded only in the arid SW: carrion (1), dung of pig (4), elephant (3), cattle (2), sheep (0); DBRU collection records from dung of cattle (11), donkey (2).

Temporal activity: Diurnal flight activity in the summer rainy season (Oct. to Apr.).

Ecoregions Namibia, Botswana: Kalahari Xeric Savanna (AT1309), Kalahari Acacia-Baikiaea Woodlands (AT0709).

Bioregions South Africa: Eastern Kalahari Bushveld (SVk), also, sand outlier in Central Bushveld (SVcb) (Savanna Biome); also in N Dry Highveld Grassland (Gh) (Grassland Biome).

Assessment rationale: EOO = 587 600 km²; no clear soil or vegetation associations despite Kalahari centre of distribution; widespread although recorded in low population density; currently assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data to assess ecological associations; protected in Witsand Nature Reserve (South Africa).

Entirely green variety.

Pale elytra variety.

Onthophagus lugubris

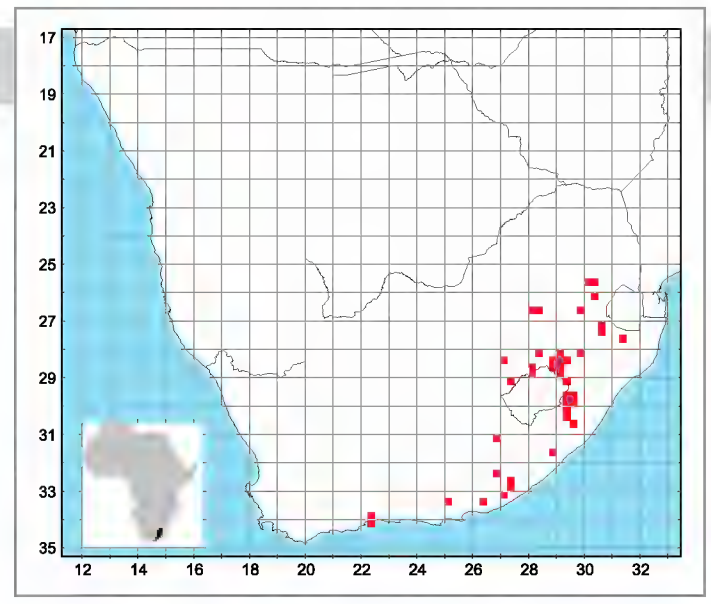
Fahraeus, 1857

= *Onthophagus lutulentus* Harold, 1867a

Global: LC (see IUCN Red List – LC)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. lugubris*: 'in terra Natalensi' [KwaZulu-Natal, South Africa]; *O. lutulentus*: invalid alternative name, postdates *O. lugubris*.
Taxonomy: Accepted Group 16 species; sexually dimorphic (head), characters vary in prominence with body size.
Distribution: From cool, moist, upland to high altitude grassland in N of range to lower-altitude upland and coastal grassland in S of range within South Africa.
Locality data (mean ± SD, range): Altitude: 1 429 ± 512, 157–2 194 m; annual rainfall: 719 ± 113, 382–960 mm; annual temperature (max. + min. /2): 14.9 ± 1.7, 11.0–18.3°C (N=47).
Habitat: No quantitative assessment; DBRU collection records primarily from finer-grained soils: sand (1), sandy loam (9), sandy clay loam (13) in pasture/grassland (20); also fallow crop fields (2).
Food types: No quantitative assessment; DBRU collection records primarily from dung of cattle (26), also horse (1), zebra (1), human/cattle mix (1).
Temporal activity: Diurnal flight activity, primarily during the summer rainy season (Oct. to May).
Bioregions South Africa: Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs), Drakensberg Grassland (Gd) (Grassland Biome); also scattered localities (possibly modified to pasture) in Albany Thicket (AT) and E Fynbos Biomes.
Assessment rationale: EOO = 180 110 km^2; recorded in low numbers at many localities in both reserves and farm pastures; difficult to assess threats due to absence of quantitative data on habitat associations, but occurrence across a wide range including fallow crop fields suggests it may currently be assessed as Least Concern LC).
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; protected in Royal Natal National Park, Ithala Game Reserve, Suikerbosrand Nature Reserve.



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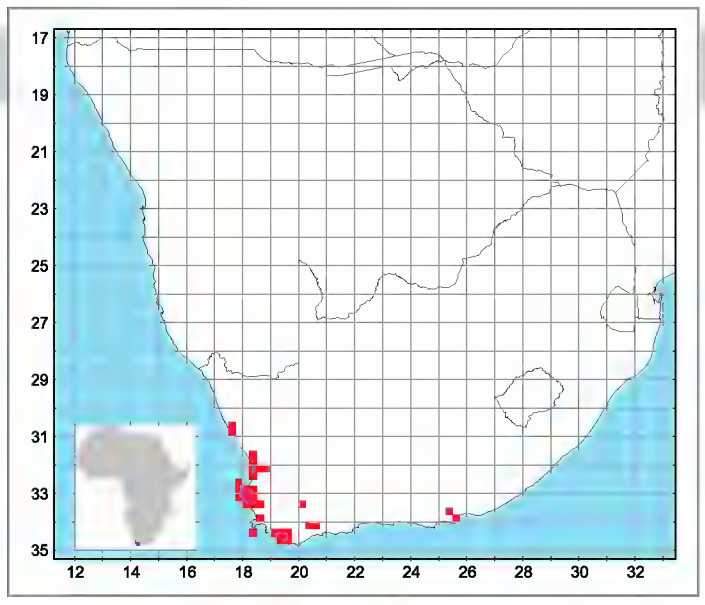


Onthophagus minutus

(Hausmann, 1807)

= *Onthophagus opacus* Fahraeus, 1857
= *Onthophagus rusticus* Boheman, 1858

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Copris minuta*: 'Vorgebirges der guten Hoffnung' [Cape of Good Hope, South Africa]; *O. opacus*: 'in terra Natalensi' [KwaZulu-Natal, South Africa]; *O. rusticus*: 'Promontorium Bonae Spei' [Cape of Good Hope, South Africa].

Taxonomy: Accepted Group 9 species; sexually dimorphic (head), prominence of characters varies with body size; synonymy of *O. opacus* requires validation as the type locality lies far outside of the known species range of *O. minutus*.

Distribution: Centred on dry, coastal and inland valley, deep sands of winter and bimodal rainfall regions, Western and Eastern Cape, South Africa; W/E disjunction possibly a mix of collection artefact and unsuitable soil (finer-grained) or climate (higher rainfall).

Locality data (mean ± SD, range): Altitude: 118 ± 146, 0–868 m; annual rainfall: 303 ± 99, 132–455 mm; annual temperature (max. + min. /2): 16.6 ± 0.9, 15.2–18.4°C (N=39).

Habitat: On West Coast in SW Western Cape: abundance high on coastal sands in moist natural shrubland (3 548–5 361), substantial in dry natural shrubland (635) and sparse grassland cleared of shrubs (586–894), low in moist Kikuyu pasture on sandy loam (32–37); on sand of Cape Peninsula: high abundance in Kikuyu pasture with high cattle density (883), low in natural shrubland with low density of herbivores (75–92); DBRU collection records primarily from deep sand (11), also sandy loam (1), sandy clay loam (1) primarily from fallow crop fields (7), also scrub/shrubland/open woodland (3), grassland cleared of shrubs (2).

Food types: No quantitative assessment; DBRU collection records from dung of cattle (12), buffalo (1), horse (1).

Temporal activity: Diurnal flight activity throughout the year except June; in Western Cape; activity peak in moist warm spring to early summer (Aug. to Dec.) becoming very low in dry summer and low in cool autumn (Jan. to May), absent in June becoming active end of July; sclerotised individuals throughout year (especially Aug. to Oct.), tenerals (Sept. to Dec.; mainly Nov.).

Bioregions South Africa: In the W: centred on Western Strandveld (F 11) in vegetation units (FS 1–3, FS 5, FS 7); also Southwest Fynbos (FO 2), Sand Fynbos vegetation units (FFd 2–5, FFd 7) (Fynbos Biome); in the E: recorded in Albany Thicket Biome (AT)

Assessment rationale: EOO = 44 485 km^2; wide EOO, but AOO presumably smaller due to sandy soil bias; abundance variable according to habitat type and density of dung; apparently somewhat tolerant of habitat transformation, which is high on coastal sands of Western Cape (FS: 25–70%; FFd: 27–80%); assessed as Least Concern (LC) owing to wide range and tolerance of transformation.

Conservation measures: Assessment of conservation status would be improved by standardised data on ecological associations; protected in West Coast National Park and Cape of Good Hope Nature Reserve.

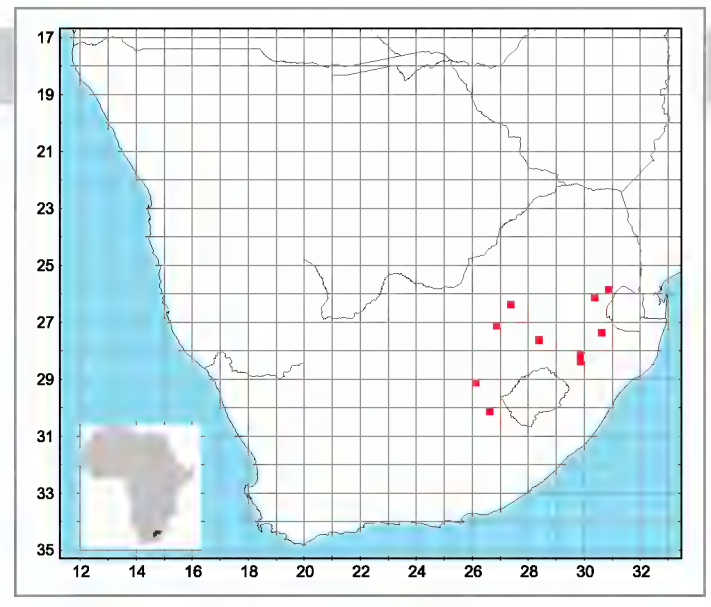
Onthophagus monodon

Fahraeus, 1857

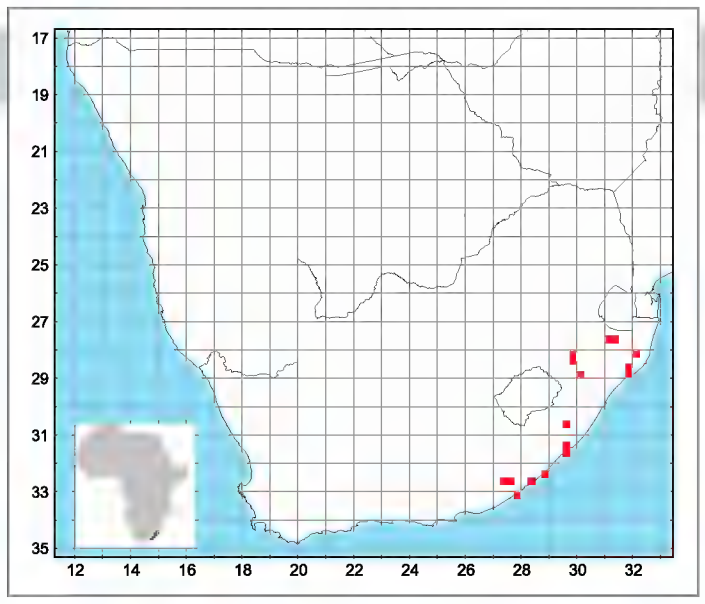
No synonyms

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: 'in terra Natalensi' [KwaZulu-Natal, South Africa].
Taxonomy: Accepted Group 9 species, but validation required by comparison with type(s); original description insufficiently clear to fully validate the species cited, here, as *O. monodon*, which is undoubtedly different to a single specimen in the National Collection of Insects labelled '*Onthophagus monodon*' and 'Natal'; colour, sheen and rugosity of interstriae ('Elytra.....nigro-violacea, nitidissima, rugulosa') in original description, better matches the species treated here as *O. monodon*; sexually dimorphic (head), characters vary in prominence with body size.
Distribution: Cool Highveld Grassland: South Africa; record from Zimbabwe requires validation (probable error).
Locality data (mean ± SD, range): Altitude: 1 416 ± 165, 1 167–1 672 m; annual rainfall: 753 ± 174, 514–1 157 mm; annual temperature (max. + min. /2): 16.3 ± 1.0, 14.5–17.4°C (N=16).
Habitat: No adequate quantitative assessment; single DBRU collection record from pasture on sandy clay loam; on sandy clay loam at Carolina: weak bias to natural *Themeda* grassland (7) compared to regenerating crop fields (4) and improved Kikuyu grass pasture (1).
Food types: No quantitative assessment; single DBRU collection record on dung of cattle; also sampled to cattle dung.
Temporal activity: Diel flight periodicity unknown; active during the summer rainy season (Nov. to Apr.).
Bioregions South Africa: Dry Highveld Grassland (Gh), Mesic Highveld Grassland (Gm), margins of Sub-Escarpment Grassland (Gs) (Grassland Biome).
Assessment rationale: EOO = 100 835 km^2; sampled at scattered localities over a wide area of the Highveld: Mpumalanga, Gauteng, KwaZulu-Natal, North-West Province, but taxonomically and ecologically poorly known; population density may be influenced by disturbance of natural grassland; assessed as Least Concern (LC) on basis of large EOO, but essentially Data Deficient (DD).
Conservation measures: Assessment of conservation status would be improved by taxonomic validation and quantitative data on ecological associations; protected in Abe Bailey Nature Reserve.



Onthophagus naso

Fahraeus, 1857

No synonyms

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'juxta fluvium Gariep' [near Orange River, South Africa – probably inexact].
Taxonomy: Accepted Group 19 species; minor sexual dimorphism (head).
Distribution: Moist coastal and lower E escarpment grasslands in the summer rainfall region of SE South Africa.
Locality data (mean ± SD, range): Altitude: 578 ± 517, 0–1 406 m; annual rainfall: 833 ± 99, 664–988 mm; annual temperature (max. + min. /2): 18.5 ± 2.1, 13.5–21.5°C (N=18).
Habitat: No adequate quantitative data; in Ithala Game Reserve: single specimens recorded on finer-grained soils in higher (1 360 m) and lower middle veld (910 m) grassland; at farm Boschberg, KwaZulu-Natal: only in middle veld grassland (9 at 1 283 m) not on Highveld (0 at 1 683 m); severely limited DBRU collection records on sandy clay loam (1), clay (1) in grassland (2).
Food types: No quantitative data; sampled to pig dung at farm Boschberg, KwaZulu-Natal; many Ditsong Museum specimens trapped to meat bait.
Temporal activity: Diel activity unknown, but active in summer rainy season (Oct. to Mar.).
Bioregions South Africa: Mainly Sub-Escarpment Grassland (Gs), (Grassland Biome); grassland in Sub-Escarpment Savanna (SVs), SE Lowveld (SVl) (Savanna Biome) and Indian Ocean Coastal Belt Biome (CB).
Assessment rationale: EOO = 70 340 km^2; would have a smaller AOO if specialisation to omnivore dung /carrion on finer-grained soils in grassland is supported; not well represented in most collections; probably a collection artefact due to food specialisation; however, sizeable range that would not be susceptible to woodland clearance if a grassland specialist; currently assessed as Least Concern (LC).
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; protected in grassland patches in Hluhluwe Game Reserve.

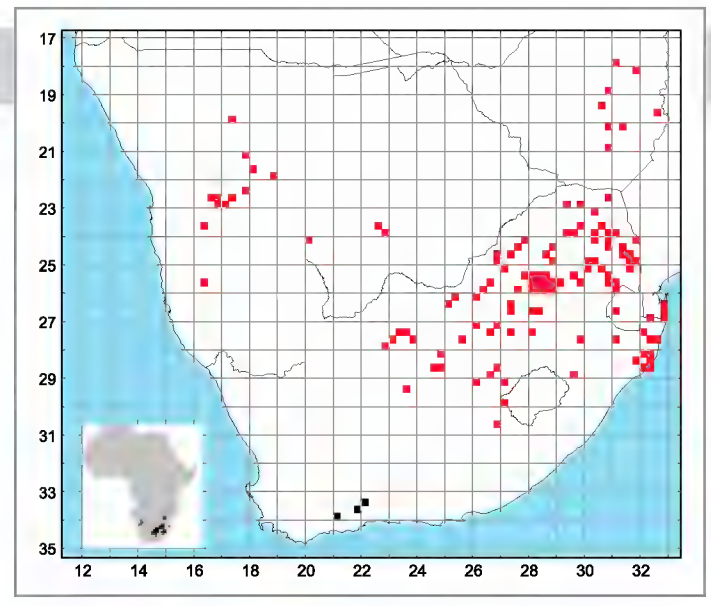
Onthophagus obtusicornis

Fahraeus, 1857

= *Onthophagus imitativus* Péringuey, 1901

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: *O. obtusicornis*: 'terra Natalensi' [KwaZulu-Natal, South Africa]; *O. imitativus*: 'Transvaal (Rustenburg)' [North-West Province, South Africa].

Taxonomy: Accepted Group 16 species; sexually dimorphic (head), characters vary in prominence with body size.

Distribution: Known disjunct distribution pattern in three main upland and coastal savanna centres in southern Africa; possibly relict outlier populations in Eastern Cape Province (black squares): South Africa, Botswana, Namibia, Zimbabwe, Mozambique; citation from Zambia requires validation.

Locality data (mean ± SD, range): Altitude: 1 014 ± 537, 0–1 998 m; annual rainfall: 634 ± 170, 128–1 100 mm; annual temperature (max. + min. /2): 19.0 ± 2.2, 14.5–23.7°C (N=179).

Habitat: Soil associations variable; in Gauteng bushveld: strong bias to sandy clay loam (3 622) compared to deep sand (263), in uMkhuze Game Reserve: bias to deep sand (0.9) and sand over clay (3.2) compared to sandy clay loam (0) and clay (0.1); in Gauteng bushveld: bias to open vegetation, grassland (2 204), open woodland (1 283), shaded thickets (398); on deep sands in Maputo Elephant Reserve: extreme bias to grassland (7.8) compared to forest (0.3); DBRU collection records: sand (18), sandy loam (20), sandy clay loam (10) in grassland/pasture (26), open shrub/woodland (21), thickets/forest (6), also crop fields (2).

Food types: Somewhat of a food generalist; in Gauteng bushveld: biased to carrion (33) and pig dung (33), also dung of horse (12), cattle (9), rotted grass clippings (1), overripe banana (5); similar bias at Phalaborwa: dung of pig (119), elephant (14) and cattle (20); DBRU collection records on dung of cattle (27), elephant (2), rhinoceros (1), zebra (2), horse (1), donkey (3), human (5), human/cattle mix (4), hyaena (1).

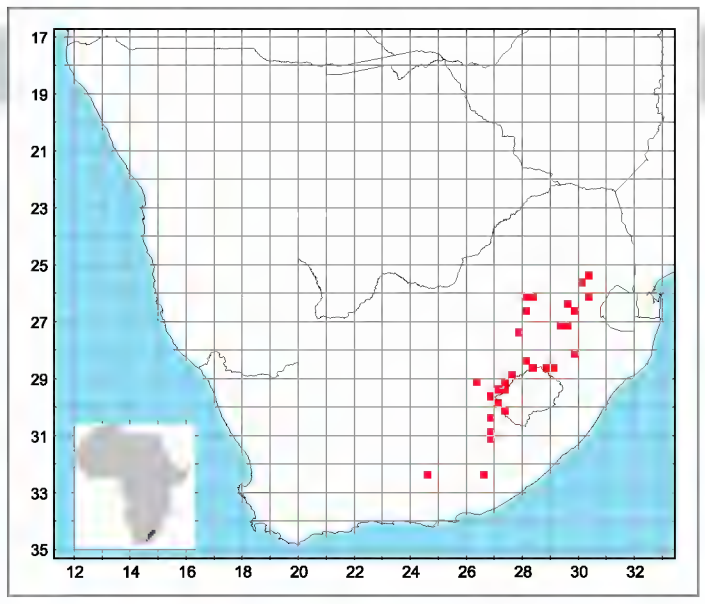
Temporal activity: Diurnal flight activity recorded throughout the year, but in Gauteng bushveld: peak activity in the summer rainy season continuing into early dry season (Oct. to May); very low activity in later dry season unless there is unseasonal rainfall (increased activity recorded after June rain); at Phalaborwa: most active on a warm sunny day after heavy rainfall (92), less so on a warm cloudy day after light rain (36) or on a hot dry sunny day (25).

Ecoregions Namibia, Botswana, Zimbabwe, Mozambique: Namibian Savanna Woodlands (AT1316), Kalahari Xeric Savanna (AT1309), Southern Miombo Woodlands (AT0719), Maputaland Coastal Forest Mosaic (AT0119).

Bioregions South Africa: Main range: Lowveld (SVl), Central Bushveld (SVcb), Eastern Kalahari Bushveld (SVk) (Savanna Biome); N Indian Ocean Coastal Belt Biome (CB); Dry Highveld Grassland (Gh), N Sub-Escarpment Grassland (Gs) (Grassland Biome).

Assessment rationale: EOO = 418 675 km^2; widespread in both farmland and reserves with a bias to open vegetation and some tolerance of habitat transformation; wide range of food types despite a bias to omnivore dung; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by further quantitative data to resolve apparent conflict in current results; occurs in various reserves including Kruger National Park and Hluhluwe–iMfolozi Game Reserve.



Onthophagus obtutus

Péringuey, 1901

No synonyms

Global: LC
Endemic: RSA, Lesotho

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. obtutus*: 'Cape Colony (Burghersdorp), Transvaal (Potchefstroom)' [South Africa: Burgersdorp, Eastern Cape; Potchefstroom, North-West Province].

Taxonomy: Accepted Group 17 species; sexually dimorphic (head and prothoracic disc), characters vary in prominence with body size.

Distribution: Cool, dry to moist, highland grassland range from NE to SW along central Highveld: South Africa; also cited from Lesotho.

Locality data (mean ± SD, range): Altitude: 1 579 ± 226, 688–2 009 m; annual rainfall: 677 ± 107, 289–924 mm; annual temperature (max. + min. /2): 15.0 ± 1.2, 12.3–19.4°C (N=33).

Habitat: No quantitative assessment; at farm Boschberg, KwaZulu-Natal: only on hills of Highveld (22 at 1 677 m) not in nearby middle veld (0 at 1 283 m), less in burnt (5) than natural grassland (17); DBRU collection records suggest bias to finer-grained soils, sand (3), sandy loam (4), sandy clay loam (14), clay (1) primarily in grassland/pasture (12), shrubland (1), also fallow crop fields (3).

Food types: No quantitative assessment; DBRU collection records entirely from cattle dung (28).

Temporal activity: Diel flight periodicity unknown, but probably diurnal during the summer rainy season (Oct. to May).

Bioregions South Africa: Centred on Mesic Highveld Grassland (Gm); marginal in edge of three other grassland bioregions (all Grassland Biome).

Assessment rationale: EOO = 89 365 km^2; AOO may be smaller if a bias to finer-grained soils is supported; range centred on a bioregion subject to 6–69% transformation in vegetation units that are 23–67% transformed, mostly above 50%; currently assessed as Least Concern (LC) owing to widespread range and occurrence at many localities.

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, particularly effects of habitat transformation since few known records are from protected areas; protected in Suikerbosrand Nature Reserve (Gauteng).

Onthophagus pallidipennis

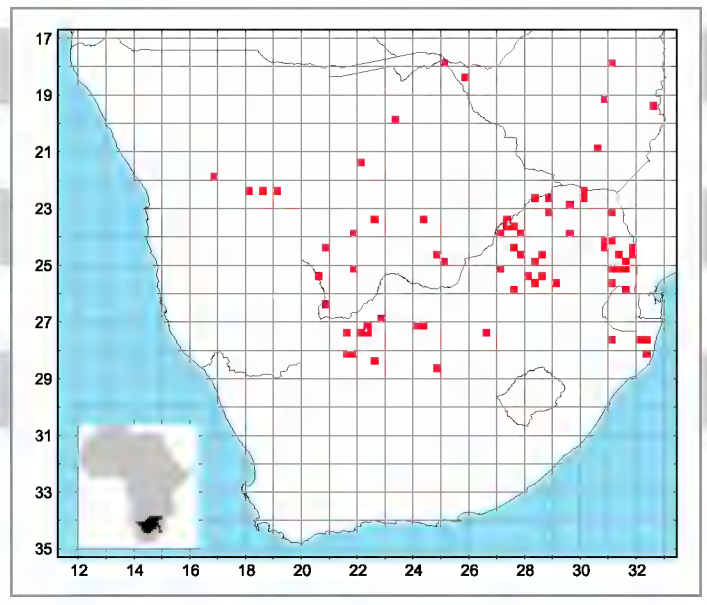
Fahraeus, 1857

Onthophagus suturalis

Péringuey, 1888

Onthophagus politissimus

d'Orbigny, 1908



Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. pallidipennis*: 'juxta fluvium Gariep' [near Orange River, South Africa]; *O. suturalis*: 'Limpopo River, Pretoria and Rustenburg, Transvaal' [South Africa: Limpopo, Gauteng and North-West provinces]; *O. politissimus*: 'Rhodésia: Salisbury' [Harare, Zimbabwe].

Taxonomy: Accepted Group 11 species, but revision required concerning status of species of similar appearance to *O. pallidipennis* that are probably unrecognised synonyms described from within its range; these species are currently regarded as valid, i.e. *O. suturalis* Péringuey, *O. politissimus* d'Orbigny, (also see notes on species account for *O. peringueyi* Shipp, 1895c).

Distribution: Dry to moist sandy savanna of central and SE southern Africa: E central Namibia, Botswana, South Africa, Zimbabwe, S Mozambique; Kenya record undoubtedly an error.

Locality data (mean ± SD, range): Altitude: 947 ± 371, 55–1 958 m; annual rainfall: 502 ± 192, 194–1 075 mm; annual temperature (max. + min. /2): 20.1 ± 1.6, 14.3–23.4°C (N=97).

Habitat: In Gauteng bushveld: extreme bias to deep sand (379) compared to sandy clay loam (4) and very strong bias to open woodland (302) compared to grassland (60) or shaded thickets (21); in uMkhuze Game Reserve: strong bias to deep sand (87.4) compared to sand over clay (25.5), sandy clay loam (18.0), clay (10.5); largely supported by DBRU collection records on sand (18), sandy loam (11), sandy clay loam (2) in grassland/pasture (9), scrub/shrubland (7), open woodland (13).

Food types: At Phalaborwa: equally abundant on dung of omnivore (pig: 173) and ruminant herbivore (cattle: 186), less so on monogastric herbivore (elephant: 22); DBRU collection records on dung of cattle (21), buffalo (1), wildebeest (1), impala (1), donkey (2), horse (2), zebra (1).

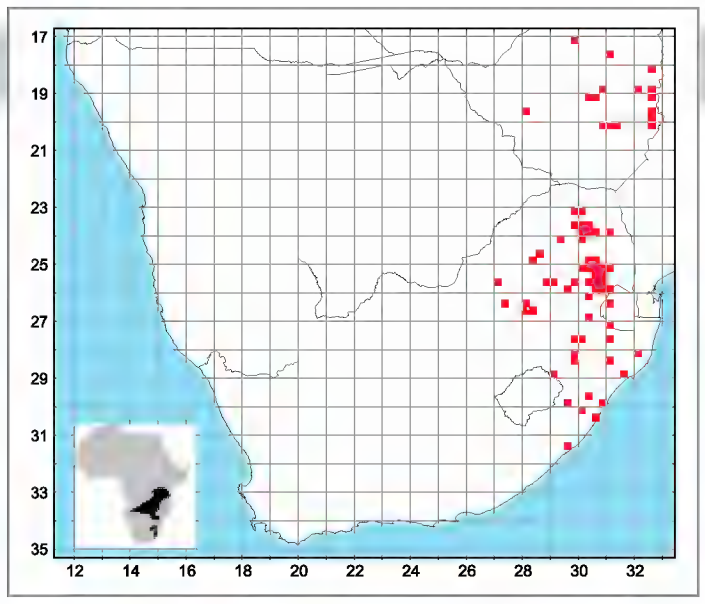
Temporal activity: Diurnal flight activity in the summer rainy season (Oct. to Apr.); in Gauteng bushveld: primarily active in early rainy season (Oct. to Dec.) declining in Jan. becoming uncommon Feb. to Apr.; at Phalaborwa: primarily active on a warm day after heavy rainfall (295), less active on a hot, dry day (66), least active on a warm cloudy day (19).

Ecoregions Namibia, Botswana, Zimbabwe: Kalahari Xeric Savanna (AT1309), Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian and Mopane Woodlands (AT0725), Zambezian Baikiaea Woodlands (AT0726), Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Lowveld (SVl), Mopane (SVmp), Central Bushveld (SVcb), Eastern Kalahari Bushveld (SVk), moister W Kalahari Duneveld (SVkd) (Savanna Biome).

Assessment rationale: EOO = 1 056 735 km^2; widespread EOO, but AOO would be smaller due to soil type bias; also, population density possibly influenced by clearance of woodland, which is extensive in parts of range; however, assessed as Least Concern (LC) owing to large EOO and protection in various reserves.

Conservation measures: Assessment of conservation status would be improved by resolution of apparent confusion in taxonomic relationships; protected in Kruger National Park, uMkhuze Game Reserve (South Africa).



Onthophagus parumnotatus

Fahraeus, 1857

= *Onthophagus parumnotatus* Fahraeus, 1857, var. *conjunctus* d'Orbigny, 1905

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. parumnotatus*: 'prope fluvium Gariep' [near Orange River, South Africa]; var. *conjunctus*: 'Afrique oriental anglaise: Boura' [Kenya: Bura].

Taxonomy: Accepted Group 16 species; sexually dimorphic (head), character varies in prominence with body size.

Distribution: Disjunct pattern; moist SE coast and N uplands of South Africa, moist upland blocks in SE and S central Africa, moist East African highlands and wet coast (Zanzibar): South Africa, Eswatini, Zimbabwe, Malawi, Angola, Kenya; also reported from Mozambique, Democratic Republic of the Congo (DRC), Rwanda, Tanzania.

Locality data (mean ± SD, range): Altitude: 1 213 ± 420, 46–2 286 m; annual rainfall: 812 ± 145, 549–1 415 mm; annual temperature (max. + min. /2): 17.5 ± 2.2, 10.6–22.0°C (N=103).

Habitat: No quantitative assessment; DBRU collection records biased to finer-grained soils: sand (5), sandy loam (11), sandy clay loam (11), clay (4) in open vegetation: pasture/grassland (23), open shrub/woodland (2), woodland (2).

Food types: No adequate quantitative assessment; in mid-altitude grassland and open woodland in Ithala Game Reserve: primarily sampled to pig dung (26) compared to cattle (6) and horse dung (1); DBRU collection records primarily from cattle dung (29), also dung of buffalo (1), horse (2), zebra (2), elephant (1), human (1), and human/cattle mix (1).

Temporal activity: Diurnal flight activity, primarily during the summer rainy season (Sept. to Apr.).

Ecoregions Zimbabwe: Southern Miombo Woodlands (AT0719), Eastern Zimbabwean Montane Forest Grassland Mosaic (AT1006).

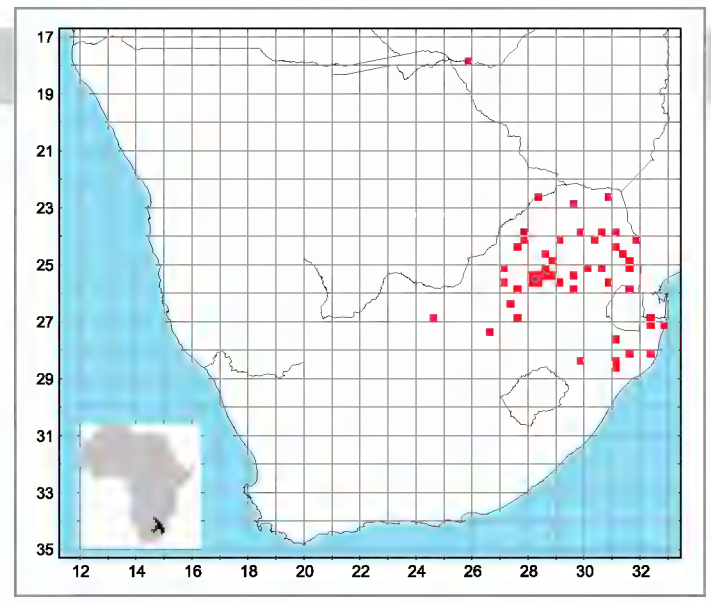
Bioregions South Africa: Primarily moist, warm edges of Mesic Highveld Grassland (Gm) (Grassland Biome) with Central Bushveld (SVcb) or Lowveld (SVl) (Savanna Biome); also N Sub-Escarpment Grassland (Gs) (Grassland Biome) and Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 2 391 165 km^2 (misleading); AOO very much smaller on finer-grained soils of moist, warm temperate to tropical uplands and wet coastal situations, hence, the disjunction between moist upland ranges in South Africa and Zimbabwe across the hot, dry Limpopo Valley; type locality presumably inaccurate as it is cited from a cooler area; not abundant, but not uncommon; primarily in open vegetation across an extensive EOO; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; protected in various nature reserves including Abe Bailey, Suikerbosrand and Vernon Crookes (South Africa).

Onthophagus pauxillus

d'Orbigny, 1902



No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'Transvaal: Hamman's Kraal près de Pretoria...; Bechouana : Vryburg' [South Africa: Hammanskraal, Vryburg].

Taxonomy: Accepted Group 10 species.

Distribution: Centred on moist, lower-altitude savanna in SE Africa: South Africa, Zimbabwe; also reported from Botswana, Mozambique.

Locality data (mean ± SD, range): Altitude: 949 ± 452, 8–1 670 m; annual rainfall: 657 ± 99, 306–897 mm; annual temperature (max. + min. /2): 19.3 ± 2.2, 14.5–23.7°C (N=67).

Habitat: In Gauteng bushveld: no significant soil bias although many more on sandy clay loam (2 624) than deep sand (798) with bias to open woodland (2 061) compared to grassland (1 164) and shaded thickets (197) (cited as *Onthophagus* sp. nr *pullus* (b)); in open woodland at Leeuwfontein Nature Reserve: occurrence biased to sand (145.3) compared to sandy loam (103.0) and stony sandy loam (95.7); DBRU collection records from various soil types: sand (2), sandy loam (5), sandy clay loam (1), clay (1) in woody vegetation: shrubland (4), open woodland (3).

Food types: At Phalaborwa: similar numbers on dung of cattle (215) and pig (163) but few on coarse-fibred elephant dung (22); supported by DBRU collection records: cattle dung (5), human/cattle dung mix (4).

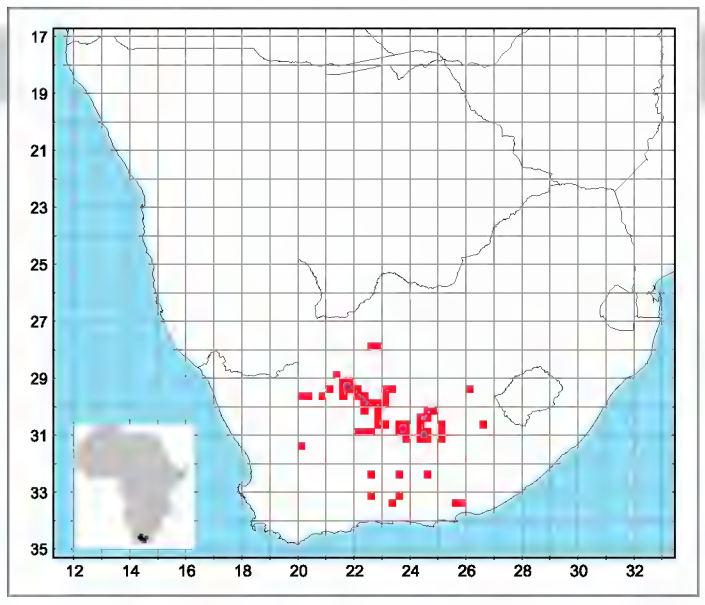
Temporal activity: Diurnal flight activity primarily during the summer rainy season (Oct. to May); in Gauteng bushveld: abundant from Oct. to Mar. with mid-dry season activity in response to unseasonal rainfall (June–July 1984); at Phalaborwa: primarily active on a warm sunny day after heavy rainfall (302) rather than on a warm cloudy day after light rainfall (64) or a hot, sunny day some time after the previous substantial rainfall (34).

Ecoregions Zimbabwe: Zambezian and Mopane Woodlands (AT0725).

Bioregions South Africa: Primarily Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome); margins of six other bioregions.

Assessment rationale: EOO = 316 435 km^2 (underestimated); small body size probably responsible for under-collection and under-estimation of EOO; often abundant with relatively generalist ecological associations; therefore, likely resilient to less-extreme forms of habitat transformation; assessed as Least Concern (LC).

Conservation measures: None recommended; protected in various nature reserves including, Leeuwfontein, Tswaing, Telperion (South Africa).



Onthophagus peringueyi

Shipp, 1895d

= *Onthophagus biplagiatus* Péringuey, 1888

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: *O. peringueyi nom nov.* for *O. biplagiatus* [pre-occupied name]: 'Beaufort West, Cape Colony' [Western Cape, South Africa].

Taxonomy: Group 11 species; treated here as a valid taxon although not formally revalidated; currently listed in error as a synonym of *Onthophagus suturalis* Péringuey, 1888, whose type localities of 'Limpopo River, Pretoria and Rustenburg', lie outside of the range of *O. peringueyi*; *O. suturalis* is, currently, listed as a valid species, but would be an unrecognised synonym of *O. pallidipennis* Fahraeus, 1857.

Distribution: Cooler S of the arid SW of Africa: South Africa; citations from Botswana are an error.

Locality data (mean ± SD, range): Altitude: 1 157 ± 243, 97–1 632 m; annual rainfall: 247 ± 74, 118–538 mm; annual temperature (max. + min. /2): 17.0 ± 1.8, 13.4–20.2°C (N=136).

Habitat: No adequate quantitative assessment; in scrub and grassland of Northern Cape: higher frequency in samples from cooler uplands to S of Orange River (5.0/sample; 90.1% frequency = 109/121) and in Upper Karoo (5.6; 95.6% = 65/68) than in hot, arid Bushmanland (0.1; 28.8% = 19/66) with no clear soil association: sand (5.5/sample), sandy loam (5.1), sandy clay loam (3.2); DBRU collection records on sand (2), sandy loam (4), sandy clay loam (5), clay (1) in grassland (1), scrub (2), shrubland (3).

Food types: No quantitative assessment; DBRU collection records on dung of cattle (9), buffalo (2), sheep (2), horse (1).

Temporal activity: Diurnal flight activity during the late summer rainy season (Jan. to May).

Bioregions South Africa: Bushmanland (NKb), Upper Karoo (NKu), Lower Karoo (NKl) (Nama Karoo Biome); Albany Thicket Biome (AT); Rainshadow Valley Karoo (SKv) (Succulent Karoo Biome); marginal in two other bioregions to NE.

Assessment rationale: EOO = 219 865 km^2; sampled with high frequency across an arid, little-transformed range used primarily for grazing of domestic livestock to whose dung it is readily attracted; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by resolution of taxonomic errors and better quantitative data on ecological associations; protected in Addo Elephant National Park.

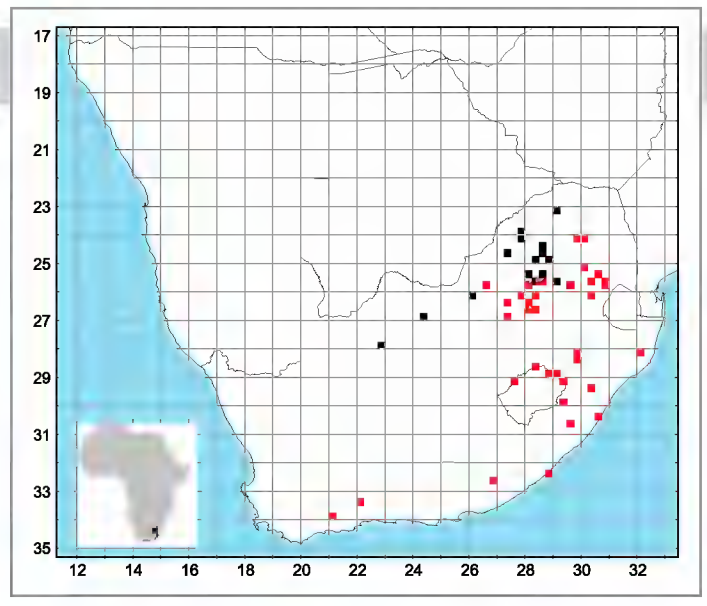
Onthophagus pilosus

Fahraeus, 1857

= *Onthophagus costipennis* Fahraeus, 1857
= *Onthophagus pellax* Péringuey, 1901

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: *O. pilosus*: 'ad Boschiesmanns Rand' [uncertain origin meaning: ?to Bushmans Ridge]; *O. costipennis*: 'juxta fluvium Gariep' [near Orange River, South Africa]; *O. pellax*: 'Transvaal (Klerksdorp)' [Klerksdorp, North-West Province, South Africa].

Taxonomy: Accepted Group 16 species, but synonymy of *O. pellax* and *O. pilosus* requires validation; aedeagi identical, but clypeal margin of putative *O. pellax* (black squares) more sinuous than that of *O. pilosus* (red squares); sexually dimorphic (head), character varies in prominence with body size.

Distribution: Apparently restricted to South Arica; *O. pilosus*: moist NE Highveld and E coastal occurrence; *O. pellax*: bushveld occurrence decreasing in population density to the SW.

Locality data (mean ± SD, range): *O. pilosus*: altitude: 1 353 ± 519, 0–2 653 m; annual rainfall: 757 ± 159, 246–1 271 mm; annual temperature (max. + min. /2): 16.2 ± 2.3, 7.9–21.3°C (N=51). *O. pellax*: altitude: 1 151 ± 150, 903–1 485 m; annual rainfall: 591 ± 75, 338–664 mm; annual temperature (max. + min. /2): 19.1 ± 1.0, 17.2–21.3°C (N=24).

Habitat: *O. pellax*: in Gauteng bushveld, extreme bias to sand (16) compared to sandy clay loam (0) with strong bias to open vegetation, grassland (13), open woodland (3), shaded thickets (0); in open woodland at Leeuwfontein Nature Reserve: sand (40), sandy loam (8), stony sandy loam (29); *O. pilosus*: on sandy loam in Abe Bailey Nature Reserve: bias to open vegetation, grassland (10.6), open woodland (3.1); on sandy clay loam at Carolina: natural *Themeda* grassland (20), regenerating vegetation on former crop fields (27), improved Kikuyu grass pasture (2).

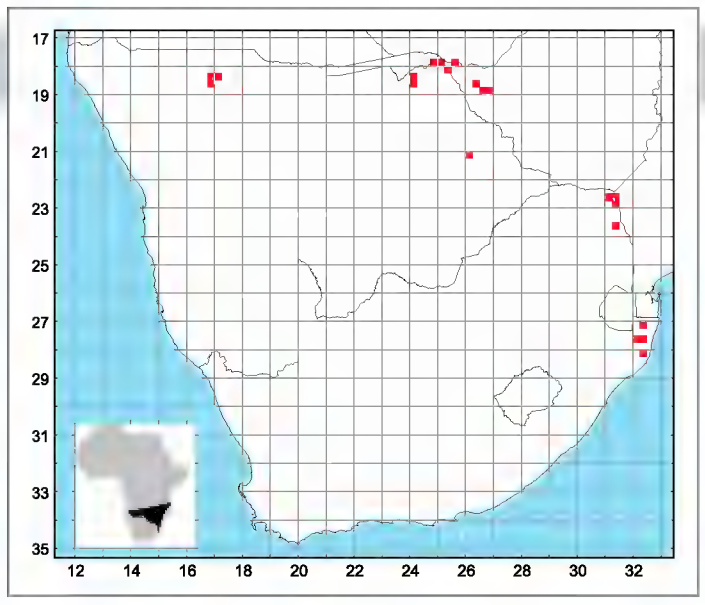
Food types: No quantitative assessment; attracted to cattle and pig dung, but no standardised comparison.

Temporal activity: Diel flight pattern unknown; active primarily in the summer rainy season (Oct. to Apr.) with July activity recorded in warmer coastal regions (Hluhluwe Game Reserve).

Bioregions South Africa: *O. pilosus*: Centred on Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs) (Grassland Biome) and Indian Ocean Coastal Belt Biome (CB), marginal occurence in five other bioregions; *O. pellax*: Central Bushveld (SVcb), Eastern Kalahari Bushveld (SVk) (Savanna Biome), also N Dry Highveld Grassland (Gh) (Grassland Biome).

Assessment rationale: EOO = 156 440 km² (*O. pilosus*), EOO = 40 975 km² (*O. pellax*); possible differences in distribution pattern and ecological associations may support two cryptic species, but further data required, particularly to determine if differences in soil association exist; large ranges, bias to open vegetation, and some resilience to disturbance suggest an overall assessment of Least Concern (LC) is justified even without taxonomic revision.

Conservation measures: Accurate assessment of conservation status requires that questions of taxonomic status should be resolved; assessment would be improved by further quantitative data on ecological associations; *O. pellax* protected in Tswaing and Leeuwfontein nature reserves, *O. pilosus* in Abe Bailey and Lekgalameetse nature reserves.



Onthophagus plebejus

Klug, 1855

= *Onthophagus stercorarius* Fahraeus, 1857

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. plebejus*: 'Sena', lectotype: 'Sinna' [= Sena, central Mozambique]; *O. stercorarius*: 'prope fluvium Gariep' [inexact, near Orange River, South Africa].

Taxonomy: Accepted Group 5 species (subgenus *Afrostrandius*); minor sexual dimorphism (head, prothoracic disc), characters vary in prominence with body size.

Distribution: Widespread in savanna of S and S central Africa, but now range restricted to game reserves, presumably due to range contraction of monogastric herbivores from whose dung most field collections have been made: NE South Africa, N Namibia, N Botswana, Zimbabwe, S Angola, Zambia, Mozambique, SE Tanzania; citation from Kenya requires validation.

Locality data (mean ± SD, range): Altitude: 654 ± 403, 55–1 207 m; annual rainfall: 619 ± 117, 379–871 mm; annual temperature (max. + min. /2): 22.6 ± 1.1, 21.1–25.7°C (N=32).

Habitat: No quantitative data; DBRU collection records from sand (8), sandy loam (7), sandy clay loam (4) in grassland (2), shrubland (1), open woodland (12).

Food types: In Botswana: strong bias to omnivore dung (pig, 71) as opposed to herbivore dung (elephant, 25; cattle, 0; sheep, 13) and carrion (chicken livers, 2); however, DBRU collection records almost exclusively from dung of monogastric herbivores: elephant (12), rhinoceros (3), horse (1); ruminant herbivore: cattle (1).

Temporal activity: Flight activity in darkness during the summer rainy season (Oct. to Apr.), also Aug. at warmer coastline; attracted to light.

Ecoregions Namibia, Botswana, Zimbabwe: Angolan Mopane Woodlands (AT0702), Zambezian and Mopane Woodlands (AT0725).

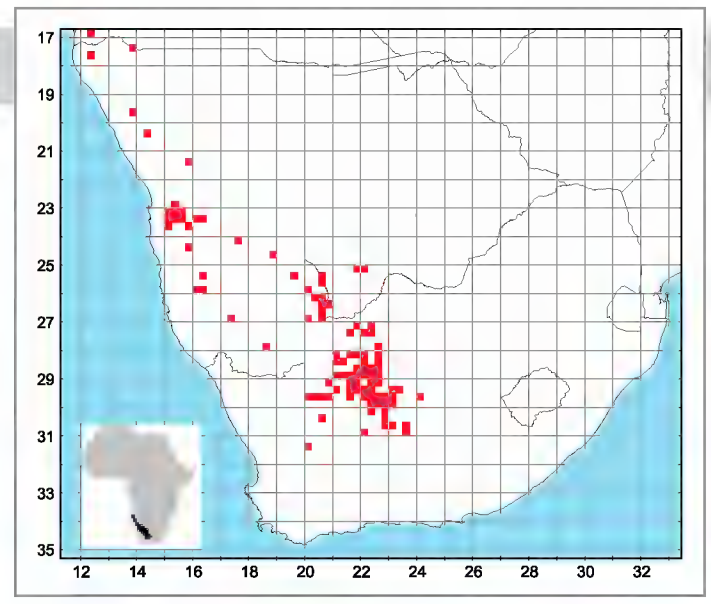
Bioregions South Africa: Mopane (SVmp), Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 1 949 910 km^2; despite a measured bias to omnivore dung, all DBRU records from game parks (23) or areas containing elephants (5); overall centring on game reserves is reflected by the mapped fragmented range; however, currently assessed as Least Concern (LC) on the basis of small, scattered AOO protected in various game reserves within a very large EOO.

Conservation measures: Assessment of conservation status would be improved by quantitative data on habitat associations, particularly if there is a bias to sandy soils and to open woodland whose clearance might have a negative impact on population density; further food association data is also required to determine if conservation of this species is tied to that of monogastric herbivores, particularly elephants, rather than to that of omnivores; protected in various national parks and game reserves including: Kruger, uMkhuze (South Africa), Hwange (Zimbabwe), Chobe (Botswana), Etosha (Namibia), Bicuar (Angola).

Onthophagus probus

Péringuey, 1901



No synonyms

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'Cape Colony (Hope Town), Mossamedes' [Hopetown, Northern Cape, South Africa; Namibe, Angola].

Taxonomy: Accepted Group 20 species.

Distribution: Arid, late summer rainfall region, SW Africa: central N South Africa, SW Botswana, W Namibia, SW Angola.

Locality data (mean ± SD, range): Altitude: 1 010 ± 195, 47–1 884 m; annual rainfall: 205 ± 63, 22–356 mm; annual temperature (max. + min. /2): 18.8 ± 1.3, 13.3–21.4°C (N=218).

Habitat: No adequate quantitative assessment; in the Northern Cape: abundance was lower in arid Bushmanland (9.9) than the moister SW Kalahari (34.6) where it was equally abundant on deep sand (38.3) and sandy loam (36.5); however, limited DBRU collection records were primarily from sand (13) rather than finer-grained soils (sandy clay loam: 1) and entirely in open vegetation: grassland (6), scrub/shrubland (6), open woodland (2).

Food types: In SW Botswana: well represented on various dung types with a slight bias to omnivore dung (pig: 544) rather than monogastric herbivore dung (228) or ruminant herbivore pads (cattle: 199) or pellets (sheep: 339), rare on carrion (chicken livers: 2); limited DBRU collection records from dung of cattle (7), wildebeest (1), horse (2).

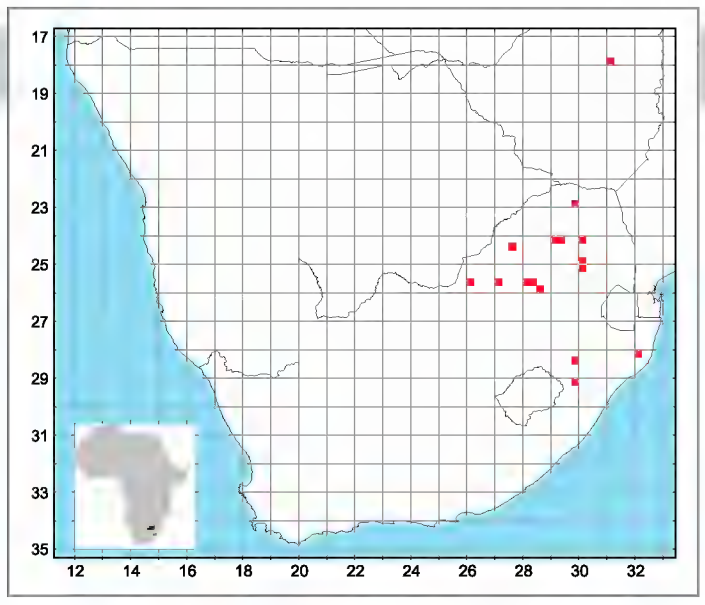
Temporal activity: Diurnal flight activity recorded throughout most of the year; abundance known to be high during the late summer rainy season (Feb. to Apr.).

Ecoregions Namibia, Botswana: Namibian Savanna Woodlands (AT1316), SW Kalahari Xeric Savanna (AT1309).

Bioregions South Africa: Bushmanland (NKb), NW Upper Karoo (NKu) (Nama Karoo Biome); Kalahari Duneveld (SVkd), W Eastern Kalahari Bushveld (SVk) (Savanna Biome).

Assessment rationale: EOO = 830 525 km^2; widespread across a little-transformed region used primarily for the grazing of farm livestock where it is attracted to a wide range of dung types; unclear if AOO is influenced by soil type; but wide expanses of various soil types occur within its EOO; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would benefit from improved quantitative data on habitat associations; protected in the Kgalagadi Transfrontier Park (South Africa/Botswana).



Onthophagus producticollis

d'Orbigny, 1908

No synonyms

Global: DD

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Natal: Estcourt' [Estcourt, KwaZulu-Natal, South Africa].

Taxonomy: Accepted Group 12 species (subgenus: *Trichonthophagus*); sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.

Distribution: Primarily finer-grained soils in moist upland savanna regions, South Africa: E–W range along N edge of Highveld, Waterberg and Soutpansberg; also lower SE escarpment, KwaZulu-Natal, South Africa, plus E central Zimbabwe; disjunctions may be a mix of collecting artefacts and regional centring of distributions.

Locality data (mean ± SD, range): Altitude: 1 283 ± 300, 273–1 736 m; annual rainfall: 719 ± 79, 587–900 mm; annual temperature (max. + min. /2): 17.5 ± 1.3, 16.2–17.3°C (N=18).

Habitat: No adequate quantitative assessment; in Gauteng bushveld: not present on deep sand (0); recorded only on sandy clay loam (13) in grassland (2), open woodland (5), shaded thicket (6); limited DBRU collection records on sand (1), sandy clay loam (2), clay (1) in pasture/grassland (4).

Food types: No quantitative assessment; limited DBRU collection records on dung of cattle (3).

Temporal activity: Putative diurnal flight activity although other Group 12 species fly in darkness; active during the summer rainy season (Nov. to Apr.).

Ecoregions Zimbabwe: Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Central Bushveld (SVcb at N edge of Highveld, Waterberg, Soutpansberg), edge of Sub-Escarpment Grassland (Gs) and Sub-Escarpment Savanna (SVs), also S Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 85 445 km^2; AOO may be more restricted due to soil, vegetation and climate type specialisations, but further quantitative support required; uncommonly recorded, therefore, difficult to determine conservation status; assessed as Data Deficient (DD), but probably Least Concern (LC) on basis of large range.

Conservation measures: Adequate assessment of conservation status requires improved quantitative data on ecological associations to determine how much smaller AOO would be compared to EOO; protected in Rustenburg Nature Reserve and Hluhluwe–iMfolozi Game Reserve (South Africa).

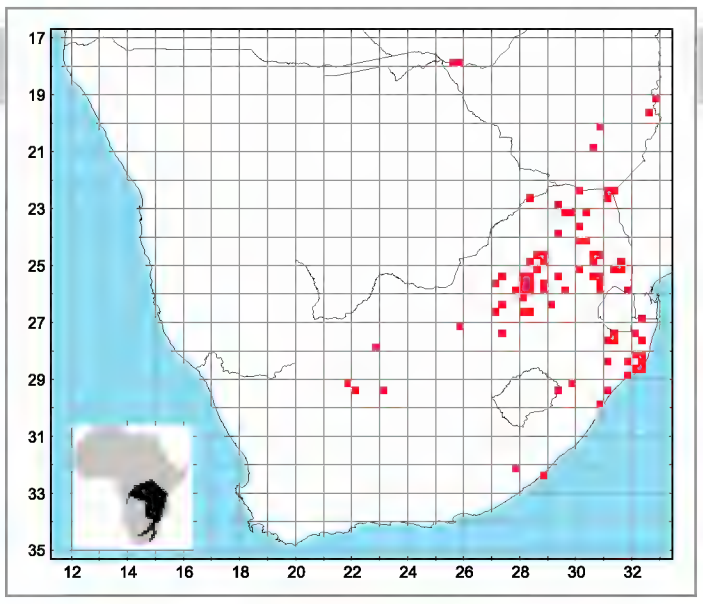
Onthophagus pugionatus

Fahraeus, 1857

= *Onthophagus pugionatus* Fahraeus, 1857, var. *latefulvus* d'Orbigny, 1902
= *Onthophagus rufaticollis* d'Orbigny, 1904
= *Onthophagus pugionatus* Fahraeus var. *rufus* d'Orbigny, 1905
= *Onthophagus pugionatus* Fahraeus, 1857 var. *quadraticornis* d'Orbigny, 1905
= *Onthophagus caucanus* Balthasar, 1939b

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: *O. pugionatus*: 'prope fluvium Gariep et in terra Natalensi' [South Africa: near Orange River and KwaZulu-Natal]; var. *latefulvus*: 'Afrique orientale allemande: Mhonda,..Zanzibar,..Haut-Zambèze,.. Nyassa,..lac Ngami' [Tanzania, S central Africa, Botswana]; *O. rufaticollis*: 'Congo: Haute Maringa' [Democratic Republic of the Congo (DRC)]; var. *rufus*: 'Afrique orientale allemande: Tanga' [Tanzania]; var. *quadraticornis*: 'Kibwezi' [Kenya]; *O. caucanus*: 'Columbien, Cauca' [Colombia: Cauca; Neotropical type locality undoubtedly an error].

Taxonomy: Accepted Group 24 species; sexually dimorphic (head, prothoracic disc), characters vary markedly in prominence with body size; also some colour pattern variation; some taxonomic re-examination, perhaps, justified.

Distribution: Widespread in moist, shaded savanna thicket and forest from S to NE Africa; also cool highland grasslands at S edge of range: South Africa, Zimbabwe, Malawi, Mozambique, Tanzania; synonyms from Botswana, Democratic Republic of the Congo (DRC), Kenya; also cited from Gabon, Angola, Namibia, Rwanda, Uganda, Ethiopia, Somalia; many records N of 15°S require validation.

Locality data (mean ± SD, range): Altitude: 916 ± 541, 0–1 824 m; annual rainfall: 714 ± 199, 213–1 394 mm; annual temperature (max. + min. /2): 19.3 ± 2.6, 14.0–25.2°C (N=129).

Habitat: In Gauteng bushveld: slight bias to deep sand (27) compared to sandy clay loam (9) with an extreme bias to shaded thicket (34) rare in open woodland (1) and grassland (1) (sampled to cattle dung); on sandy clay loam at Roodeplaat Nature Reserve (1 254–1 288 m): thickets (113), open woodland (35), grassland (19) (sampled to composite pig/cattle dung); on sandy loam at Abe Bailey Nature Reserve (1 496–1 541 m): open woodland (28), grassland (4); supported by DBRU collection records from sand (7), sandy loam (5), sandy clay loam (4), clay (1) in thicket/forest (21), shrub/woodland (4), grassland/pasture (5).

Food types: No quantitative data; DBRU collection records biased to omnivore dung: human/cattle or buffalo mix (15), human (4), baboon (1) compared to herbivore dung: cattle (7), buffalo (1), wildebeest (1), zebra (1), horse (1), warthog (1).

Temporal activity: Flight activity in darkness (18:00–20:00) primarily during the summer rainy season (Oct. to May), also Aug. at warmer coast.

Ecoregions Zimbabwe: Shaded situations in Zambezian and Mopane Woodlands (AT0725), Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Primarily moister SE Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome), Indian Ocean Coastal Belt Biome (CB); also E and N margins of four bioregions in Grassland Biome plus rare records in dry bioregions along Orange River, Northern Cape.

Onthophagus pugionatus (continued)

Assessment rationale: EOO = 4 391 285 km^2 (gross estimate based on limited available data); AOO would be much smaller, largely according to vegetation offering shade; with such a bias, population density would be excessively reduced by clearance of dense woody vegetation over most of its range; high tranformation across main part of range in South Africa (0–58% (SVl); 2–49% (SVcb)); however, extremely widespread so assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by further quantitative data on ecological associations with a design that takes apparent dung and vegetation bias into consideration; protected in various national parks, game and nature reserves with dense vegetation offering shade including Kruger, Hluhluwe–iMfolozi, Roodeplaat (South Africa), Lake Mutirikwe, Victoria Falls (Zimbabwe).

Onthophagus pullus

Roth, 1851

= *Onthophagus brevicornis* Fahraeus, 1857
= *Onthophagus infuscatus* Raffray, 1877
= *Onthophagus schimbanus* Harold, 1886

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. pullus*: 'Tigré in N. Abyssinien' [Tigray, N Ethiopia]; *O. brevicornis*: 'prope fluvium Limpopo' [near Limpopo River, southern Africa]; *O. schimbanus*: *nom nov.* for *O. infuscatus* (pre-occupied name): 'vom Berge Schimba' [Shimba Mts, SE Kenya].

Taxonomy: Accepted Group 10 species, but further validation of synonyms described from Ethiopia and South Africa would be useful; sexually dimorphic (head), character varies in prominence with body size.

Distribution: Woody savanna from S to NE to W Africa: South Africa, Namibia, N Botswana, Zimbabwe, Mozambique, Kenya, Ethiopia; also cited from Malawi, Democratic Republic of the Congo (DRC), Tanzania, Somalia, Eritrea; West African citations (Gabon, Gambia, Senegal) and occurrences (Ghana, Côte d'Ivoire) should be validated.

Locality data (mean ± SD, range): Altitude: 852 ± 478, 0–1 815 m; annual rainfall: 636 ± 224, 306–1 254 mm; annual temperature (max. + min. /2): 20.1 ± 2.4, 15.4–24.8°C (N=46).

Habitat: In Gauteng bushveld: extreme bias to deep sand (443) compared to sandy clay loam (2) with strong bias to shade or partial shade: shaded thickets (318), open woodland (105), grassland (32) (cited as *Onthophagus* sp. a); supported by DBRU collection records on sand (2) in open woodland (1), woodland (1), forest (2).

Food types: No quantitative assessment; DBRU collection records from dung of human (1), human/cattle or buffalo mix (3).

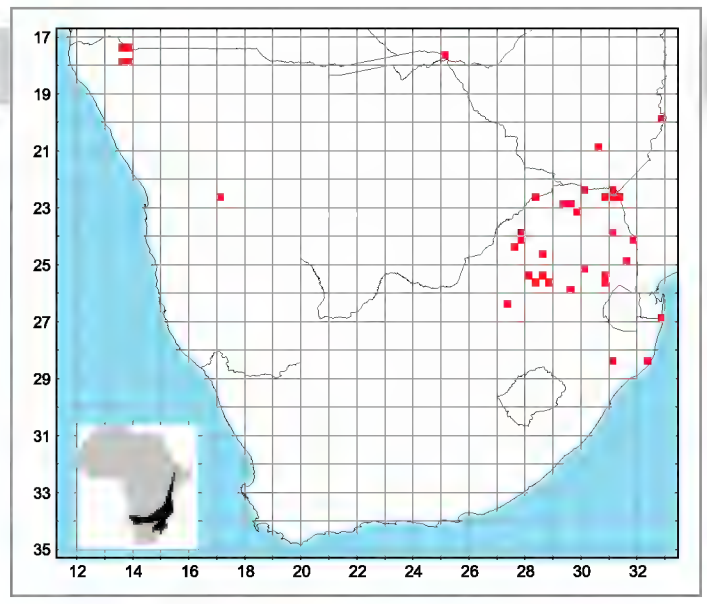
Temporal activity: Diurnal flight activity, primarily in the summer rainy season (Oct. to May); in Gauteng bushveld: abundant Oct. to Mar., numbers falling off steeply Apr. and May.

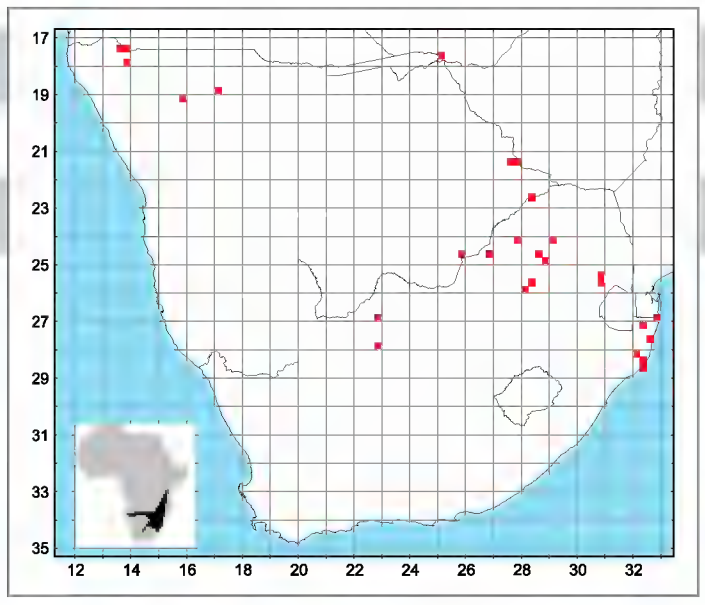
Ecoregions Namibia, Zimbabwe: N Namibian Savanna Woodlands (AT1316), Kalahari Xeric Savanna (AT1309), Zambezian and Mopane Woodlands (AT0725).

Bioregions South Africa: Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome); N Indian Ocean Coastal Belt Biome (CB); N margins Grassland Biome (Mesic Highveld Grassland (Gm), Dry Highveld Grassland (Gh)).

Assessment rationale: EOO = 2 692 290 km² (gross estimate of range restricted to type origins in S, E and NE Africa); widespread, but possibly poorly understood taxonomically; AOO in South Africa, probably smaller due to soil and vegetation specialisation; clearance of woody vegetation offering shade on sandy soils probably detrimental to population density although does occur in low numbers in open situations; therefore, assessed as Least Concern (LC).

Conservation measures: Taxonomic revision would be useful to determine if *O. pullus* comprises a single widespread species or a species complex; quantitative data on food type association required to support apparent bias to omnivore dung; protected in Kruger National Park (South Africa).





Onthophagus quadrimaculatus

Raffray, 1877

Onthophagus quadrinotatus

d'Orbigny, 1905

No synonyms

Global: DD

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. quadrimaculatus*: 'Zanguebar. Montagnes de Schimba' [Shimba Mts, SE Kenya]; *O. quadrinotatus*: 'Kibwézi' [Kibwezi, Kenya].

Taxonomy: Both accepted Group 2 species that need to be validated as distinct taxa or revised as synonyms; minor colour pattern variation in coastal individuals considered intraspecific; minor sexual dimorphism (head), character varies in prominence with body size.

Distribution: Recorded from savanna of South Africa, Botswana, Namibia, Zimbabwe, Mozambique; *O. quadrimaculatus*: cited from Kenya, Tanzania, Malawi, Zimbabwe, Mozambique; *O. quadrinotatus*: cited only from Kenya.

Locality data (mean ± SD, range): Altitude: 827 ± 449, 0–1 430 m; annual rainfall: 618 ± 195, 306–1 003 mm; annual temperature (max. + min. /2): 20.3 ± 1.8, 17.4–24.4°C (N=34).

Habitat: In Gauteng bushveld: strong bias to finer-grained soils (deep sand: 4; sandy clay loam: 14) and shaded vegetation (grassland: 0; open woodland: 0; shaded thicket: 18); severely limited DBRU collection records: sandy loam (3) on grass verges (2), open woodland (1).

Food types: No quantitative assessment; limited DBRU collection records on dung of cattle (1), dog (2), dead tenebrionid beetle (1); long series from Nylsvlei sampled to meat, faeces and banana bait.

Temporal activity: Diel flight perodicity unknown; active in the summer rainy season (Oct. to Apr.).

Ecoregions Namibia, Botswana: N Namibia Savanna Woodlands (AT1316); Angolan Mopane Woodlands (AT0702), Kalahari Acacia-Baikiaea Woodlands (AT0709), Southern African Bushveld (AT0717), Zambezian and Mopane Woodlands (AT0725).

Bioregions South Africa: Eastern Kalahari Bushveld (SVk), Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome); N Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 1 875 455 km² (gross estimate); difficult to assess conservation status given taxonomic uncertainties and limited ecological data; may be an omnivore dung/carrion specialist, but supporting quantitative data required; strong association with shade would suggest possible threats from clearance of woody vegetation; assessed as Data Deficient (DD) although putative widespread range would suggest an assessment of Least Concern (LC) would be justified.

Conservation measures: Taxonomic study of these two species and related taxa is required before an adequate assessment may be made of conservation status in conjunction with improved data on ecological associations, particularly food; protected in Nylsvlei Nature Reserve (South Africa).

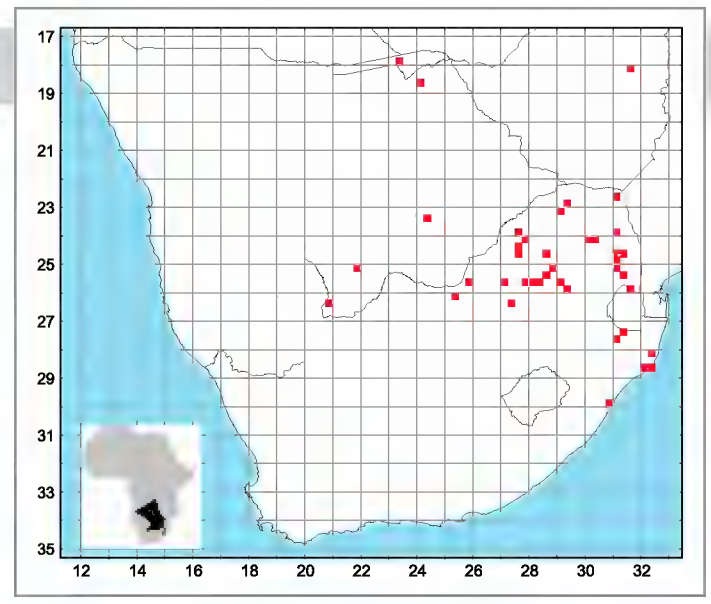
Onthophagus quadrinodosus

Fahraeus, 1857

= *Onthophagus truncaticornis* Boheman, 1860
= *Onthophagus trucidatus* Harold, 1870

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: *O. quadrinodosus*: 'in terra Natalensi' [KwaZulu-Natal, South Africa]; *O. truncaticornis* Boheman: 'juxta lacum N'Gami' [near Lake Ngami, Botswana]; *O. trucidatus*: *nom nov.* for *O. truncaticornis* Boheman [pre-occupied name].

Taxonomy: Accepted Group 12 species (subgenus: *Trichonthophagus*), sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.

Distribution: Primarily moist woody savanna on sandy soils in southern Africa: South Africa, NE Namibia, Botswana, Zimbabwe, Angola; also cited from Malawi, Democratic Republic of the Congo (DRC); citations from Somalia, Ethiopia, seem unlikely and require validation.

Locality data (mean ± SD, range): Altitude: 955 ± 450, 0–1 640 m; annual rainfall: 676 ± 168, 194–1 010 mm; annual temperature (max. + min. /2): 19.5 ± 1.9, 15.4–23.3°C (N=52).

Habitat: In Gauteng bushveld: extreme bias to deep sand (542) compared to sandy clay loam (4) and to woody vegetation, shaded thicket (295), open woodland (235) compared to grassland (16); in open woodland at Leeuwfontein Nature Reserve: sand (30), sandy loam (5), stony sandy loam (0); DBRU collection records from sand (3), sandy loam (5) in grassland (5), open shrub/woodland (3).

Food types: In Gauteng bushveld: strong bias to omnivore dung (pig, 86) rather than herbivore dung (horse, 12; cattle, 14), rare on carrion (2); DBRU collection records from dung of cattle (3), elephant (2).

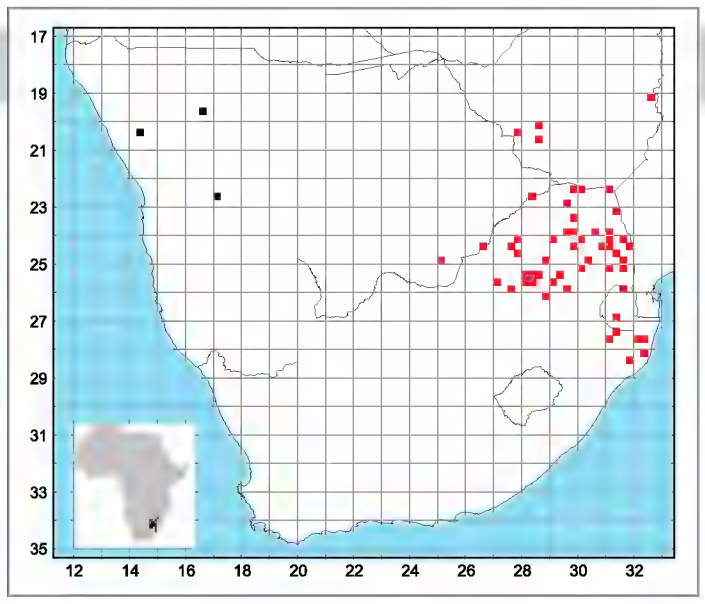
Temporal activity: Flight activity in darkness during the summer rainy season (Oct. to May); in Gauteng bushveld: little activity until Dec. continuing to Mar., tailing off steeply to early May; in Gauteng bushveld: only evening flight on cooler early and late summer nights (18:00–20:00 in Nov., Feb., Mar.), both evening and dawn flight in warmer mid-summer (18:00–20:00, 04:00–06:00 in Dec.).

Ecoregions Namibia, Botswana, Zimbabwe: SE Kalahari Xeric Savanna (AT1309), Zambezian and Mopane Woodlands (AT0725); Zambezian Baikiaea Woodlands (AT0726); Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome); Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 2 016 665 km² (gross underestimate); AOO would be smaller owing to soil and vegetation specialisation; bias to woody vegetation suggests that clearance of woodland would adversely influence population density; transformation across South African range: 0–58% (SVl), 2–49% (SVcb); however, assessed as Least Concern (LC) owing to large EOO and occurrence in both farmland and reserves.

Conservation measures: None recommended as long as woodland savanna is conserved within its range; protected within Kruger National Park (South Africa).



Onthophagus rasipennis

d'Orbigny, 1908

= *Onthophagus pallidipennis* Fahraeus, 1857, *sensu* d'Orbigny, 1902

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'Rhodésia: Bulawayo..., monts Matopos...; Transvaal: Shilouvane près de Leydsdorp...; Makapan près de Pietersburg...; Hamman's Kraal près de Pretoria' [Zimbabwe: Bulawayo and Matopos; South Africa: Shiluvane, Makapan and Hammanskraal]; *O. pallidipennis sensu* d'Orbigny, 1902: No locality stated.

Taxonomy: Accepted Group 11 species; difficult to separate from close relative, *Onthophagus pallidipennis* Fahraeus, 1857, with whose body size range it overlaps.

Distribution: Primarily finer-grained soils in moist, lowland woodland savanna, SE Africa: South Africa, Eswatini, E Botswana, Zimbabwe, Mozambique (red squares); W populations, characterised by dark area in centre of elytra, may represent a variety or a further species: N Namibia (black squares).

Locality data (mean ± SD, range): Altitude: 811 ± 457, 48–1 784 m; annual rainfall: 655 ± 129, 306–1 145 mm; annual temperature (max. + min. /2): 20.0 ± 2.1, 14.6–24.4°C (N=73) (SE populations only).

Habitat: In Gauteng bushveld: bias to finer-grained soils, sandy clay loam (15), deep sand (6) and partial shade, grassland (2), open woodland (15), shaded thicket (4); partly supported by DBRU collection records on sand (6), sandy loam (9), sandly clay loam (1), clay (1) in grassland/pasture (2), shrubland (3), open woodland (11).

Food types: No quantitative assessment; DBRU collection records on a wide range of dung types: impala (1), cattle (12), wildebeest (1), donkey (2), horse (2), zebra (1) elephant (2), human/cattle mixture (2).

Temporal activity: Diurnal flight activity in the summer rainy season (Oct. to Apr.).

Ecoregions Botswana, Zimbabwe: SE Kalahari Xeric Savanna (AT1309), E Kalahari Acacia-Baikiaea Woodlands (AT0709), Southern African Bushveld (AT0717), Southern Miombo woodlands (AT0719).

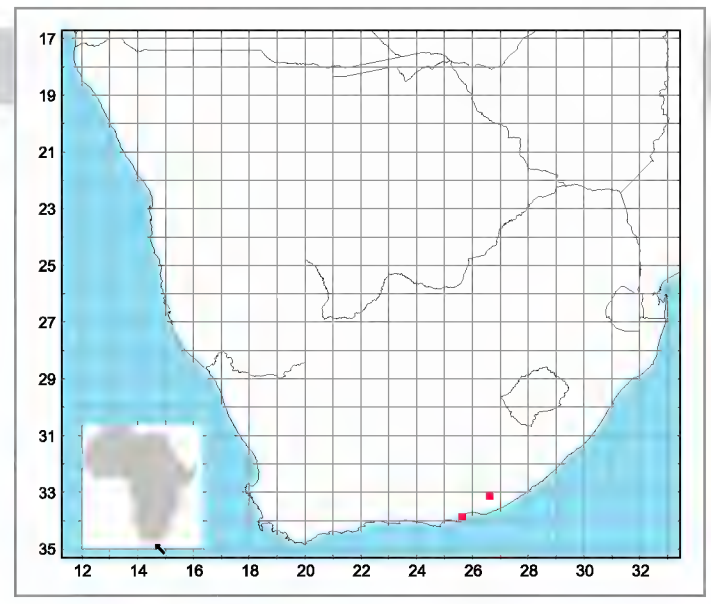
Bioregions South Africa: Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome); marginal in two other bioregions.

Assessment rationale: EOO = 230 805 km^2 (SE populations only); AOO may be smaller owing to possible soil type bias; widely distributed in savannas of SE Africa, but bias to partially shaded habitat suggests population density would be reduced by clearance of woodland; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by further quantitative data on ecological associations; protected in uMkhuze Game Reserve, Kruger National Park (South Africa).

Onthophagus scapularis

d'Orbigny, 1902

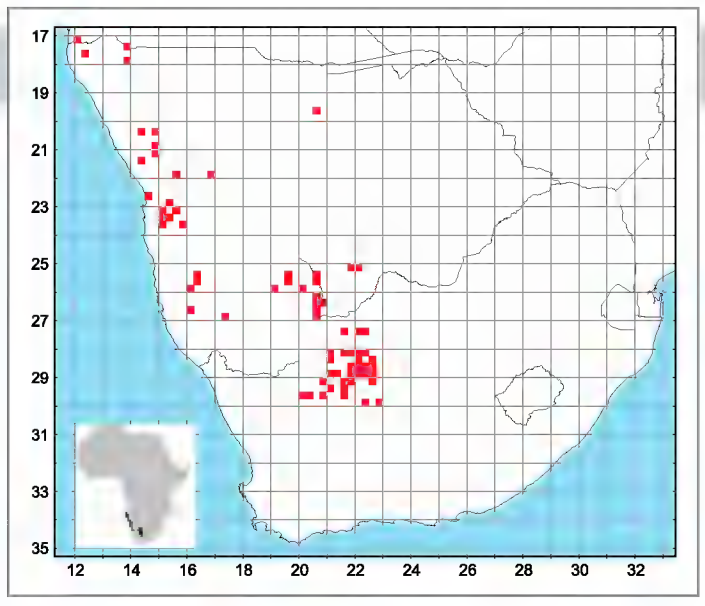


No synonyms

Global: DD
Endemic: RSA

| J | A | S | O | N | D | J | F | M | A | M | J |

Type locality: 'Colonie du Cap: Port-Elizabeth' [Eastern Cape, South Africa].
Taxonomy: Accepted Group 18 species.
Distribution: Coastal lowlands, SE Eastern Cape, South Africa, at the E limits of the bimodal rainfall region.
Locality data (mean ± SD, range): Altitude: 233 ± 232, 69–397 m; annual rainfall: 493 ± 54, 455–531 mm; annual temperature (max. + min. /2): 17.6 ± 0.0, 17.6–17.6°C (N=2).
Habitat: Not known.
Food types: Not known.
Temporal activity: Not known.
Bioregions South Africa: Albany Thicket Biome (AT).
Assessment rationale: EOO = 1 725 km² (presumably underestimated); extremely poorly known, but probably carrion-associated like other close relatives in Group 18; apparent rarity and small known range possibly a collection artefact related to food specialisation; assessed as Data Deficient (DD).
Conservation measures: Assessment of conservation status will only be possible following a quantitative survey centred on SE coastal regions of the Eastern Cape; this should determine the EOO, AOO and ecological associations; not currently known from any protected area.



Onthophagus semiflavus

Boheman, 1860

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'in vicinitate fluvii svakop' [in the vicinity of the Swakop River, W central Namibia].

Taxonomy: Accepted Group 11 species.

Distribution: Centred on the N and centre of the arid, late summer rainfall region, SW Africa: N central South Africa, SW Botswana, primarily W Namibia, SW Angola.

Locality data (mean ± SD, range): Altitude: 966 ± 229, 47–1 407 m; annual rainfall: 210 ± 77, 14–428 mm; annual temperature (max. + min. /2): 19.0 ± 1.5, 14.2–21.8°C (N=109).

Habitat: No quantitative assessment; in Northern Cape: greater frequency at study sites in arid SW Kalahari (67.3%, 66 out of 98) than in Bushmanland (32.8%, 22 out of 67) or Karoo to S of Orange River (8.1%, 10 out of 121); DBRU collection records entirely from sand (15) in grassland/pasture (5), scrub/shrubland (8), open woodland (2).

Food types: In Botswana: attracted to various dung types with a bias to omnivore dung: pig (2 527), elephant (1 000), cattle (813), sheep (1 128), rare on carrion (1); DBRU collection records from dung of cattle (5), wildebeest (1), horse (1), donkey (3).

Temporal activity: Diurnal flight activity during the late summer rainy season (Dec. to May) with additional records during winter and spring, probably from warmer regions.

Ecoregions Namibia, Botswana: Namib Desert (AT1315), Namibian Savanna Woodlands (AT1316), SW Kalahari Xeric Savanna (AT1309); marginal in Kaokoveld Desert (AT1310), N Succulent Karoo (AT1322), Kalahari Acacia-Baikiaea Woodlands (AT0709).

Bioregions South Africa: Bushmanland (NKu) (Nama Karoo); Kalahari Duneveld (SVkd), W Eastern Kalahari Bushveld (SVk) (Savanna Biome).

Assessment rationale: EOO = 226 630 km^2; AOO may be smaller if specialisation to sandy soils is shown, but currently no supporting quantitative data; attracted to various dung types across a large arid range where land usage is primarily conservation or grazing in little-transformed habitat; therefore, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on habitat associations; protected in Kgalagadi Transfrontier Park (Botswana and South Africa).

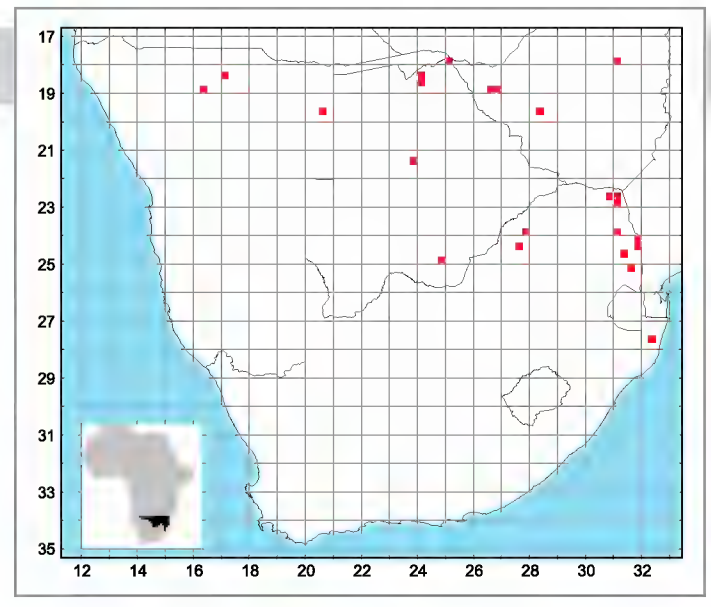
Onthophagus suffusus

Klug, 1855

= *Onthophagus crucifer* Klug, 1855

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: *O. suffusus*: 'Inhambane' [Mozambique]; *O. crucifer*: 'Sena' [central Mozambique].

Taxonomy: Accepted Group 31 species (subgenus *Furconthophagus*); sexually dimorphic (head); characters vary in prominence with body size.

Distribution: Widespread in dry to moist southern African savanna, but now mostly localised to game reserves: South Africa, Mozambique, Zimbabwe, Botswana, Namibia; also cited from Angola, Malawi.

Locality data (mean ± SD, range): Altitude: 719 ± 403, 55–1 410 m; annual rainfall: 586 ± 113, 362–835 mm; annual temperature (max. + min. /2): 21.8 ± 1.4, 18.6–25.7°C (N=31).

Habitat: No adequate quantitative assessment; at South African Wildlife College in Kruger National Park: no soil bias, finer-grained gabbro-derived soils (101.4), coarse-grained granite-derived soils (92.1), but fewer in nearby communal rangeland, gabbro-derived (12.3), granite-derived (11.4); limited DBRU collection records from sand (4) and sandy loam (3) only in open woodland (7).

Food types: On deep sand in the moister NE of Botswana: sampled to various dung types, but with a distinct bias to omnivore dung (pig, 851) compared to monogastric (elephant, 396) or ruminant herbivore dung (cattle, 153; sheep, 25), or carrion (213); similar bias at Phalaborwa: dung of pig (741), elephant (105), cattle (5); limited DBRU collection records from dung of cattle (3), elephant (3), human/cattle mix (1).

Temporal activity: Flight activity in darkness primarily during the summer rainy season (Sept. to Mar.); at Phalaborwa: more active on a warm evening following light rainfall (437), fewer on evenings during hot, dry weather (210) or during warm weather following heavy rainfall (206).

Ecoregions Namibia, Botswana, Zimbabwe: Angolan Mopane Woodlands (AT0702), Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian and Mopane Woodlands (AT0725), Zambezian Baikiaea Woodlands (AT0726), Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 962 255 km² (underestimated); despite a measured bias to omnivore dung, most available records out of 34 were close to (7) or within (24) game reserves, which accounts for the scattered distribution pattern; thus, AOO would be much smaller than EOO; soil data inconclusive and bias to woody vegetation unsupported quantitatively; however, owing to wide range and abundance within a number of reserves, assessed as Least Concern (LC).

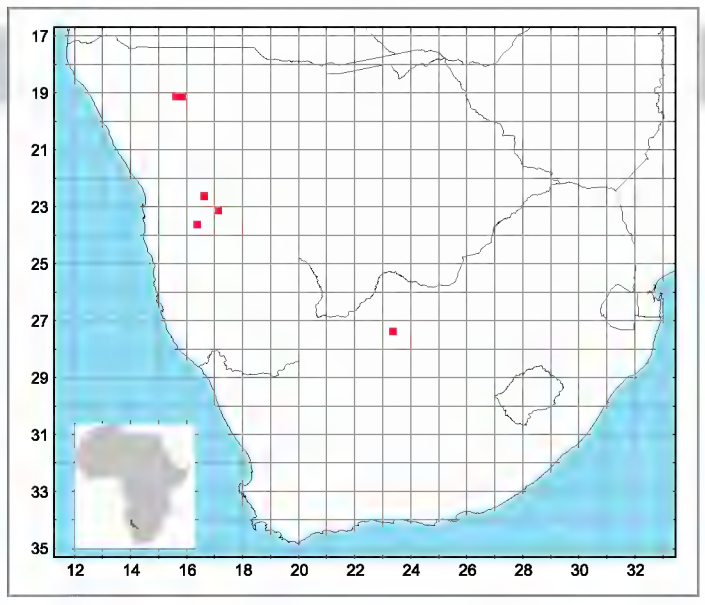
Conservation measures: Assessment of conservation status would be improved by quantitative data to determine if there is a bias to sandy soils and woody vegetation; also to determine if the distribution pattern represents range contraction into game reserves driven by range contraction of indigenous monogastric herbivores despite conflicting food association data; protected in various national parks including: Kruger (South Africa), Chobe (Botswana), Hwange (Zimbabwe).

♂

2 mm

♀

2 mm



Onthophagus tricorniger

Boheman, 1860

No synonyms

Global: DD
Endemic: South Africa, Namibia, ?Botswana

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'prope lacum N'Gami et in regione fluvii Svakop' [inexact: near Lake Ngami, Botswana, and in Swakop River region, central Namibia].

Taxonomy: Accepted Group 12 species, but needs to be validated by comparison with close relative or synonym, *O. tenuigraniger* d'Orbigny, 1913 (type locality (single specimen): 'Rhodésia: rivière Mpuzi dans le Manica' [inexact: Mpudzi River, Zimbabwe]); distribution of individuals treated here as *O. tricorniger* better match the type localities.

Distribution: Dry SW African savanna of the late summer rainfall region: South Africa, Namibia, Botswana; Botswana type locality (inexact) requires validation.

Locality data (mean ± SD, range): Altitude: 1 430 ± 248, 1 140–1 712 m; annual rainfall: 333 ± 85, 184–409 mm; annual temperature (max. + min. /2): 19.2 ± 2.3, 16.7–22.2°C (N=6).

Habitat: No quantitative assessment; limited DBRU collection records: biased to finer-grained soils, sand (1), sandy loam (2), sandy clay loam (3) in low profile woody vegetation, scrub (2), shrubland (3), open woodland (1).

Food types: No quantitative assessment; limited DBRU collection records on dung of cattle (4), wildebeest (1), zebra (1).

Temporal activity: Diel flight periodicity unknown; active during the late summer rainy season (Jan., Feb.).

Ecoregions Namibia: Namibian Savanna Woodlands (AT1316), NW Kalahari Xeric Savanna (AT1309), Angolan Mopane Woodlands (AT0702).

Bioregions South Africa: Eastern Kalahari Bushveld (SVk) (Savanna Biome).

Assessment rationale: EOO = 65 590 km^2 (underestimated); recorded from scattered localities across a large area in the late summer rainfall region of SW Africa; probably not currently threatened, but poorly known taxonomically and ecologically; therefore, assessed as Data Deficient (DD).

Conservation measures: Attention needs to be paid to taxonomic issues with nomenclature; a survey to determine full EOO and quantitative data on ecological associations are required before an assessment may be made of conservation status; protected in Etosha National Park (Namibia).

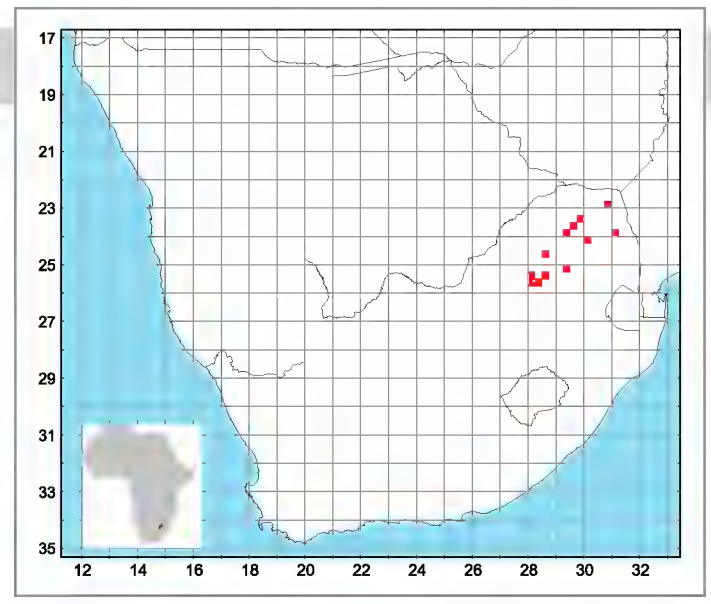
Onthophagus trinodosus

Fahraeus, 1857

No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: 'juxta fluvium Limpopo' [near Limpopo River, southern Africa].

Taxonomy: Accepted Group 16 species; minor sexual dimorphism (head prothoracic disc), characters vary in prominence with body size.

Distribution: Bushveld at N and NW edge of South African Highveld; currently considered endemic to South Africa; citation from Mozambique requires validation.

Locality data (mean ± SD, range): Altitude: 1 020 ± 272, 406–1 311 m; annual rainfall: 635 ± 88, 491–871 mm; annual temperature (max. + min. /2): 19.2 ± 1.7, 16.9–23.1°C (N=14).

Habitat: No adequate quantitative assessment; in Gauteng bushveld: recorded as a rarity only in grassland (2) and open woodland (2) on sandy clay loam (Roodeplaat), no records on deep sand (Boekenhoutskloof); but in Tswaing Nature Reserve: sampled on various soil types in grassland (8), shrubland (15), open woodland (3), shaded thicket (1); limited DBRU collection records on sandy loam (3) in grassland (1), shrubland (1), open woodland (1).

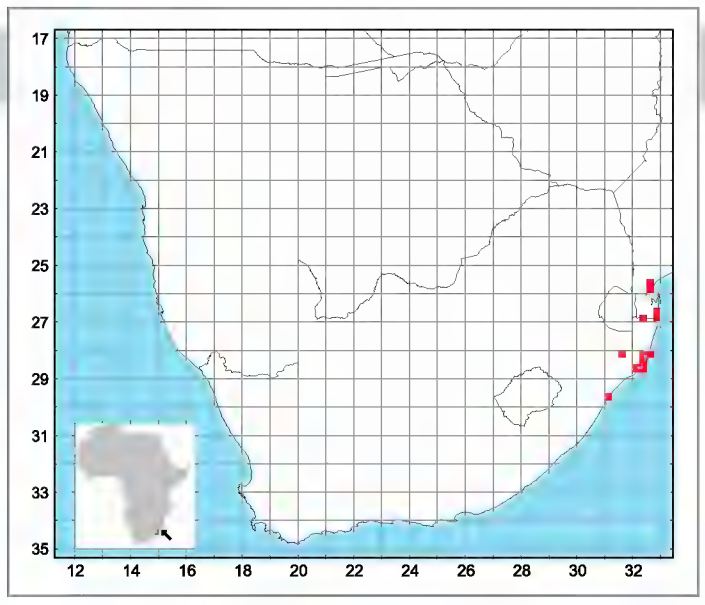
Food types: No adequate quantitative assessment; over 15 months sampling to cattle dung at Roodeplaat: recorded as a rarity (4); on a single occasion in Tswaing Nature Reserve: sampled in greater numbers to composite pig/cattle dung baits (27); limited DBRU collection records on cattle dung (3).

Temporal activity: Diel flight periodicity unknown; active during the summer rainy season (Oct. to Feb.), one record in June.

Bioregions South Africa: SE Central Bushveld (SVcb); single records in Lowveld (SVl), Mopane (SVmp) (Savanna Biome).

Assessment rationale: EOO = 32 470 km^2; poorly known species; sizeable, but fairly restricted range; recorded only in very low numbers bar for samples from Tswaing Nature Reserve; transformation 17–49% across SVcb part of range, but available data inadequate for determining conservation status; assessed as Data Deficient (DD).

Conservation measures: Improved quantitative data on ecological associations are required before conservation status may be assessed; protected in Tswaing Nature Reserve.



Onthophagus ursinus

d'Orbigny, 1902

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'Mozambique: Delagoa.....Natal' [Maputo, Mozambique; KwaZulu-Natal, South Africa].

Taxonomy: Accepted Group 12 species (subgenus: *Trichonthophagus*).

Distribution: Moist deep sands along the SE coast from Tongaat, South Africa, at least to Beira, central Mozambique.

Locality data (mean ± SD, range): Altitude: 39 ± 76, 0–319 m; annual rainfall: 861 ± 158, 654–1 275 mm; annual temperature (max. + min. /2): 22.2 ± 1.0, 20.7–24.6°C (N=17).

Habitat: No quantitative assessment of soil association; across a gradient of rehabilitating vegetation on deep sand at Richards Bay: absent from highly shaded, dense, early succession woodland (9–12 yr) and natural dune forest; present in less-shaded, early succession shrubland (6 yr: 1.7) and more open later succession woodland (15–24 yr: 0.1–1.2); most abundant in least shaded, early succession grassland (0 yr: 7.2) and open senescent late succession woodland with many fallen trees (27 yr: 15.8); limited DBRU collection records entirely on sand (3) in pasture (1), shrubland (1), open woodland (1).

Food types: No quantitative assessment; limited DBRU collection records entirely on cattle dung (3).

Temporal activity: Diel flight periodicity unknown; active in the summer rainy season (Oct. to Apr.) with records also from the dry season (July).

Ecoregions Mozambique: Maputaland Coastal Forest Mosaic (AT0119), Southern Zanzibar-Inhambane Coastal Forest Mosaic (AT0128).

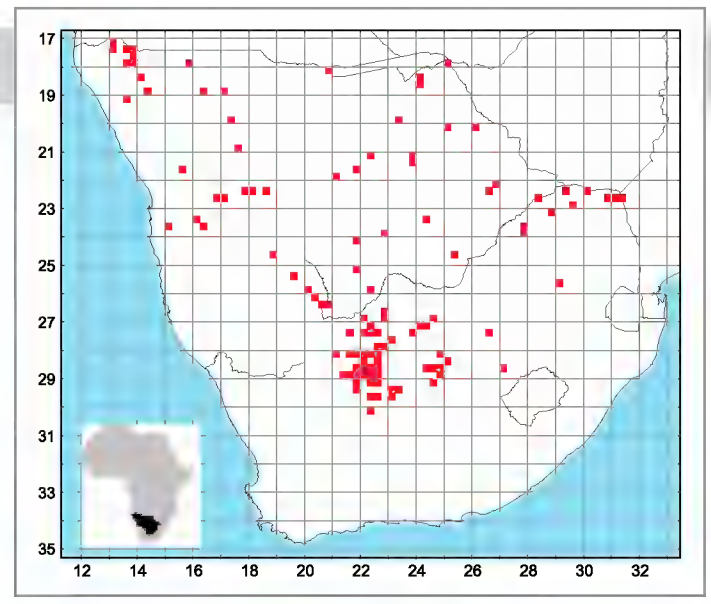
Bioregions South Africa: N Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 38 715 km^2; difficult to assess owing to limited ecological data; probably a coastal deep sand specialist in moist open vegetation although further quantitative support is required; because of apparent vegetation bias and fairly extensive range, currently assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; protected in Sileza Game Reserve and Tembe Elephant Park (South Africa).

Onthophagus venustulus

Erichson, 1843



See Taxonomy section.

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Angola' [also cited from Senegal and Egypt by Erichson].

Taxonomy: Status of *O. venustulus* dependent on whether or not the ?disjunct Kalahari populations of southern Africa are regarded as a valid Group 31 species (subgenus *Furconthophagus*); or a synonym of *O. variegatus* (Fabricius, 1798) (= current valid status), a species with a Saharo–Sindian distribution pattern from Senegal to Pakistan/Afghanistan that is also cited from coastal East Africa; sexually dimorphic (head), characters vary in prominence with body size; this variation may be why the type description of males cites two horns on the vertex instead of the three borne by major males; identity of this species requires validation.

Distribution: Southern African populations: dry savanna on S Kalahari deep sands extending to the middle Limpopo Valley and as a rarity in SE sand outliers: Angola, Namibia, Botswana, Zimbabwe, South Africa; citation from Lesotho probably an error.

Locality data (mean ± SD, range): Altitude: 1 084 ± 228, 328–1 815 m; annual rainfall: 329 ± 119, 34–690 mm; annual temperature (max. + min. /2): 19.6 ± 1.5, 15.9–23.7°C (N=184).

Habitat: No adequate quantitative assessment; in Northern Cape: frequency and abundance high in SW Kalahari (89.8% of samples, 88 out of 98; 85.1/sample on sand, 80.4 on sandy loam), low in Bushmanland (8.8%, 5/67; 0.04/sample) and uplands to S of Orange River (7.4%, 9/121; 0.3/sample); DBRU collection records indicate bias to coarse-grained soils: sand (19), sandy loam (5), sandy clay loam (2) in grassland (5), scrub/shrubland (9), open woodland (11).

Food types: In Botswana: bias to dung of omnivores (pig, 434) and monogastric herbivores (elephant, 324) compared to ruminant herbivores (cattle, 84; sheep, 48) and carrion (chicken livers, 72); however, DBRU collection records entirely from cattle dung (28).

Temporal activity: Flight activity during darkness, primarily in the summer rainy season (Sept. to Apr.).

Ecoregions Namibia, Botswana: Namibian Savanna Woodlands (AT1316), Kalahari Xeric Savanna (AT1309), Kalahari Acacia-Baikiaea Woodlands (AT0709); marginal in Zambezian Baikiaea Woodlands (AT0726), Angolan Mopane Woodlands (AT0702) Zambezian and Mopane Woodlands (AT0725) and one other ecoregion.

Bioregions South Africa: Primarily, Kalahari Duneveld (SVkd), Eastern Kalahari Bushveld (SVk), sands of N Mopane (SVmp) in Limpopo Valley, rare in sand outliers of Central Bushveld (SVcb) (Savanna Biome), also N extremes Bushmanland (NKb), Upper Karoo (NKu) (Nama Karoo Biome).

Assessment rationale: EOO = 1 414 010 km^2 (underestimated, Kalahari populations only); AOO possibly smaller according to distribution of sandy soils, but requires quantitative support; large part of range coincides with little-transformed, arid areas used primarily for conservation and grazing of farm livestock, assessed as Least Concern (LC).

Conservation measures: Taxonomic issues need to be resolved; assessment of conservation status would be improved by formal quantitative data on habitat associations; protected in Kgalagadi Transfrontier Park (South Africa/Botswana), Central Kalahari Game Reserve, Chobe National Park (Botswana).

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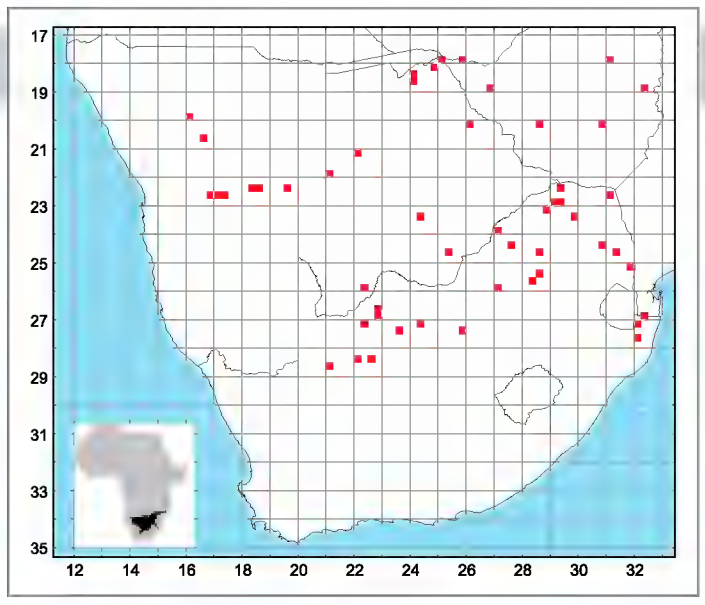


Onthophagus verticalis

Fahraeus, 1857

= *Onthophagus haroldi* Péringuey, 1888
= *Onthophagus hector* Shipp, 1895c
= *Onthophagus corniculatus* Reiche, 1847 *sensu* Péringuey, 1901

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. verticalis*: 'juxta fluvium Gariep' [near Orange River, South Africa]; *O. hector*: *nom nov.* for *O. haroldi* Péringuey (pre-occupied name): 'Potchefstroom, Transvaal, and Zambesi River' [North-West Province, South Africa; inexact, Zimbabwe]; *O. corniculatus sensu* Péringuey: recorded from 'Natal (Estcourt), Transvaal (Potchefstroom, Rustenburg), Southern Rhodesia (Victoria Falls, Middle Limpopo), Ovampoland (Omrromba)' [South Africa, Zimbabwe, Namibia].

Taxonomy: Accepted Group 12 species (subgenus: *Trichonthophagus*); sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.

Distribution: Widespread on sandy soils in dry to moist savanna of southern Africa: South Africa, Namibia, Botswana, Zimbabwe, Mozambique.

Locality data (mean ± SD, range): Altitude: 1 045 ± 415, 58–1 958 m; annual rainfall: 520 ± 178, 160–1 220 mm; annual temperature (max. + min. /2): 20.2 ± 1.8, 14.3–23.4°C (N=65).

Habitat: In Gauteng bushveld: extreme bias to deep sand (60) compared to sandy clay loam (0) with a bias to woody vegetation: grassland (6), open woodland (22), shaded thicket (32); similar soil bias in uMkhuze Game Reserve: deep sand (1.4), sand on clay (0.7), sandy clay loam (0.3), clay (0); supported by DBRU collection records on sand (15), sandy loam (9), clay (1) in grassland (7), scrub/shrubland (6), open woodland (11).

Food types: In Botswana: attracted to various dung types with a bias to monogastric herbivore (elephant, 87) and omnivore dung (pig, 64) compared to ruminant herbivore dung (pellet-dropping sheep, 37; pad-dropping cattle, 11), not recorded on carrion (0); DBRU collection records on dung of cattle (15), buffalo (2), elephant (5), horse (1), donkey (2).

Temporal activity: Flight activity during darkness in the summer rainy season (Oct. to Apr.); in Gauteng bushveld: mid-summer flight activity peaks close to dawn (04:00–06:00, Nov. to Jan.), lower abundance for evening flight activity (18:00–20:00).

Ecoregions Namibia, Botswana, Zimbabwe: Kalahari Xeric Savanna (AT1309), Kalahari Acacia-Baikiaea Woodlands (AT0709), Angolan Mopane Woodlands (AT0702), Zambezian and Mopane Woodlands (AT0725), Zambezian Baikiaea Woodlands (AT0726), Southern Miombo Woodlands (AT0719).

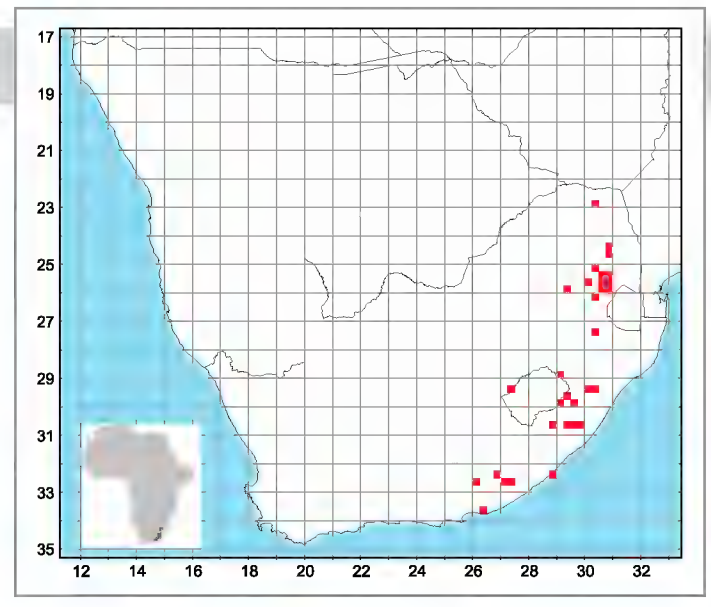
Bioregions South Africa: Eastern Kalahari Bushveld (SVk), Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 1 288 690 km^2; AOO undoubtedly somewhat smaller due to bias to sandy soils; measured bias to woody vegetation suggests clearance of woodland would be detrimental to population density in transformed areas in the NE of its range; transformation: 0–58% (SVl), 2–49% (SVcb); however, assessed as Least Concern (LC) on basis of wide EOO and protection in reserves.

Conservation measures: None recommended; protected in several national parks and game reserves including Kruger, Ndumo (South Africa), Chobe (Botswana).

Onthophagus vigens

Péringuey, 1901



No synonyms

Global: LC (see IUCN Red List – LC)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Transvaal (Lydenburg)' [Mashishing, Mpumalanga, South Africa].

Taxonomy: Accepted Group 17 species, but should be compared to *Onthophagus simillimus* d'Orbigny, 1913, described from Chirinda Forest, Zimbabwe; sexually dimorphic (head), character varies in prominence with body size.

Distribution: South Africa: from cool, moist, high altitude, forest and grassland in N of range (E edge of Highveld) to lower-altitude upland grassland and coastal forest in S of range (central SE Eastern Cape).

Locality data (mean ± SD, range): Altitude: 1 367 ± 462, 112–2 274 m; annual rainfall: 834 ± 168, 482–1 271 mm; annual temperature (max. + min. /2): 15.4 ± 2.3, 10.6–22.8°C (N=44).

Habitat: No adequate quantitative assessment; along a 500–2 800 m altitudinal gradsect from the coast to the Sani Pass, KwaZulu-Natal: recorded in grassland only at 1 500 m (0.8) and 1 900 m (1.0); DBRU collection records entirely on finer-grained soils: sandy loam (3), sandy clay loam (8), clay (1) in pasture/grassland (10) or forest (2).

Food types: No quantitative assessment; DBRU collection records primarily from cattle dung (8), also human/cattle dung mix (1).

Temporal activity: Diurnal flight activity, primarily during the summer rainy season (Oct. to May).

Bioregions South Africa: Patchy records centred on E Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs) and Drakensberg Grassland (Gd) (Grassland Biome) with records from encompassed forest types, including Northern Afrotemperate (FOz 2), Southern (FOz 3) and Northern Mistbelt (FOz 4) and Scarp Forest (FOz 5); also Southern Coastal Forest (FOz 6).

Assessment rationale: EOO = 61 695 km²; AOO probably smaller according to occurrence of suitable cool moist grassland and forest patches, but survey is required to improve the locality data; all known collection records from finer-grained soils; because of protection of some forest and grassland areas across its wide range, currently assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, particularly relative bias to soil type or bias to forest or grassland, as these remain unknown; protected in the uKhahlamba Drakensberg Park (World Heritage Site).

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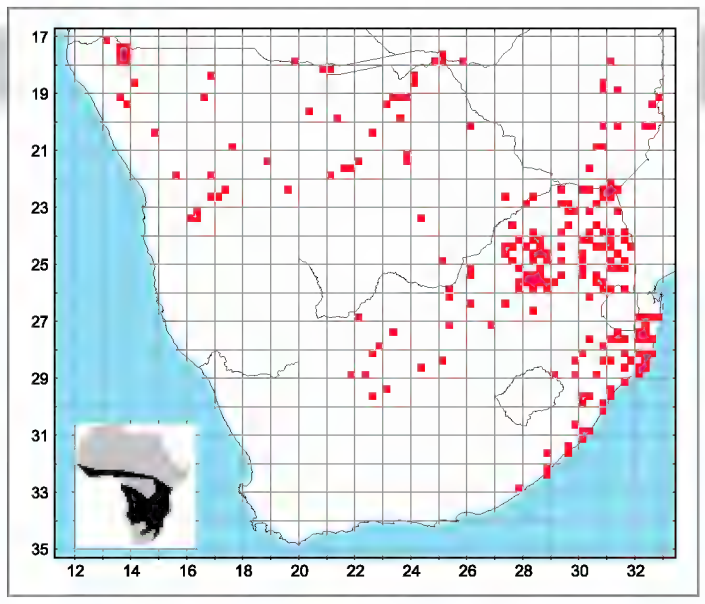


Onthophagus vinctus

Erichson, 1843

= *Onthophagus obesus* Fahraeus, 1857

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *O. vinctus*: 'Angola'; *O. obesus*: 'terra Natalensi' [KwaZulu-Natal, South Africa].

Taxonomy: Accepted Group 7 species; *O. vinctus* complex recently subdivided into three species, thus reducing known distribution from 34 to 25 African countries; limited sexual dimorphism (head, prothoracic disc).

Distribution: Widespread, mainly on sandy soils, in dry, lowland, wooded savanna and moist coastal regions from southern to E to W Africa: recorded in 25 countries from Guinea (Bissau) to Somalia to Angola, Namibia, Botswana, Zimbabwe, Mozambique and South Africa.

Locality data (mean ± SD, range): Altitude: 797 ± 487, 0–2 274 m; annual rainfall: 663 ± 234, 125–1 659 mm; annual temperature (max. + min. /2): 20.2 ± 2.2, 10.6–25.7°C (N=305).

Habitat: In Gauteng bushveld: extreme bias to deep sand (9 090) compared to sandy clay loam (20) and a bias to shaded thickets (6 253) compared to open woodland (2 229) and grassland (628); in uMkhuze Game Reserve: bias to deep sand (7.6) compared to duplex sand over clay (1.5), sandy clay loam (0) and clay (1.9); on deep sands in Botswana: primarily in the moister wooded NE (3 608) not the arid SW (3); partial support from DBRU collection records: sand (36), sandy loam (14), sandy clay loam (14) in pasture/grassland (22), shrub/woodland (29) or thicket/forest/plantation (10).

Food types: In Gauteng bushveld: primarily attracted to pig dung (1 245), much less abundant on horse (69) and cattle dung (58) or carrion (10); in Botswana: mainly dung of pig (2 269), also elephant (671), sheep (595), less on cattle (57) and carrion (16); DBRU collection records reflect commonly sampled dung types: cattle (44) and a wide range of others, human (2), baboon (1), human/cattle mix (7), elephant (6), rhinoceros (2), hippopotamus (1), zebra (2), horse (1) donkey (2), buffalo (5), wildebeest (1), waterbuck (1).

Temporal activity: In Gauteng bushveld: flight activity primarily at dusk (87–99%) from 18:00–20:00 (Nov.–Mar.); recorded throughout the year, but primarily active from end of the dry season till end of the summer rainy season (Sept. to Apr.); attracted to light.

Ecoregions Namibia, Botswana, Zimbabwe: Namibian Savanna Woodlands (AT1316), NW Kalahari Xeric Savanna (AT1309), Angolan Mopane Woodlands (AT0702), Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian and Mopane Woodlands (AT0725), Southern African Bushveld (AT0717), Southern Miombo Woodlands (AT0719), Zambezian Baikiaea Woodlands (AT0726).

Bioregions South Africa: Primarily Central Bushveld (SVcb), Lowveld (SVl), Mopane (SVmp), but also Eastern Kalahari Bushveld (SVk) (Savanna Biome); Indian Ocean Coastal Belt Biome (CB); marginal in Sub-Escarpment Grassland (Gs), N Dry Highveld Grassland (Gh) (Grassland Biome).

Assessment rationale: EOO = 8 771 775 km^2; AOO influenced by soil and vegetation bias; clearance of woodland would be detrimental to population density, but very wide EOO; in a study at Phalaborwa: recorded primarily in disturbed mine habitats; therefore, assessed as Least Concern (LC).

Conservation measures: None required; widespread, abundant and tolerant of disturbance; recorded in both farmland and protected areas including Kruger National Park (South Africa).

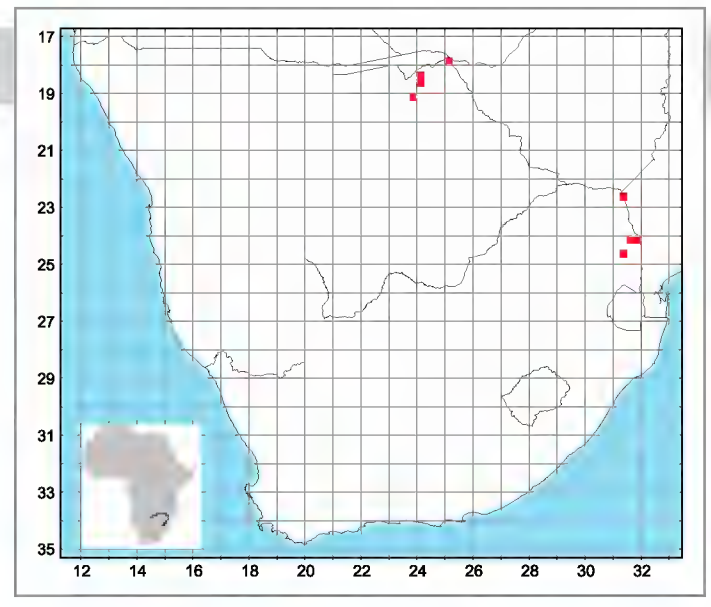
Onthophagus virescens

Harold, 1867c

= *Onthophagus nitidulus* Klug, 1855

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: *O. virescens*, *nom nov.* for *O. nitidulus* (pre-occupied name): 'Sena' [central Mozambique].

Taxonomy: Accepted Group 11 species; name requires validation, but species characteristics match the redescription in d'Orbigny (1913); sexually dimorphic (head, disc of prothorax), characters vary in prominence with body size.

Distribution: Lowland savanna on sandy soils, particularly deep sand patches, on the S Mozambique Coastal Plain and up the Zambezi Valley: NE South Africa, Mozambique, N Botswana; also cited from Zimbabwe; north Botswana populations need to be validated by further comparison with an unidentified species recorded in southwest Zimbabwe and north Namibia.

Locality data (mean ± SD, range): Altitude: 572 ± 345, 59–1 000 m; annual rainfall: 651 ± 160, 487–1 136 mm; annual temperature (max. + min. /2): 22.6 ± 1.3, 21.5–25.7°C (N=14).

Habitat: No quantitative assessment; nine out of 16 records on deep sand in savanna; limited abundance recorded on sandy loam.

Food types: On deep sand in Botswana: strong bias to omnivore dung (470) compared to herbivore dung (elephant: 106; cattle: 14; sheep: 145), rare on carrion (chicken livers: 2); limited DBRU collection records from dung of elephant (2).

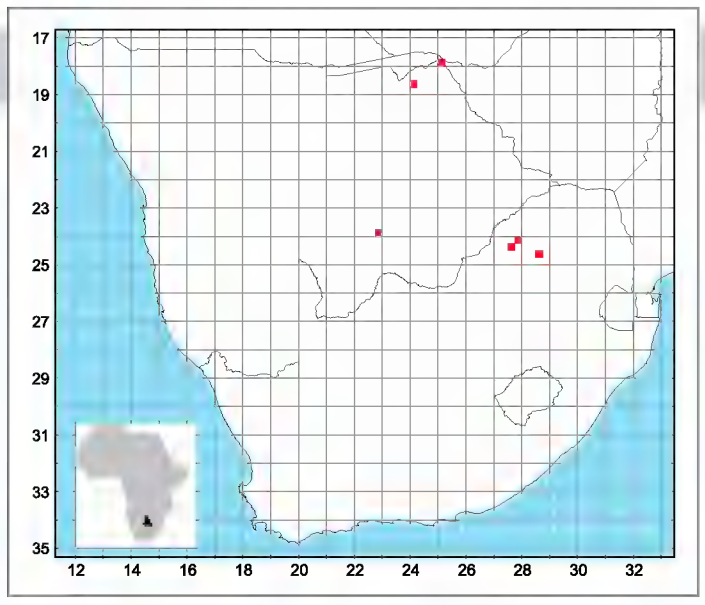
Temporal activity: Diurnal flight activity in the summer rainy season (Nov. to Apr.).

Ecoregions Botswana: Zambezian and Mopane Woodlands (AT0725), Zambezian Baikiaea Woodlands (AT0726)

Bioregions South Africa: Lowveld (SVl), Mopane (SVmp) (Savanna Biome).

Assessment rationale: EOO = 137 725 km^2 (gross estimate); large EOO, but AOO would probably be much smaller according to distribution of sandy soils in the SE, although quantitative support is required; only patchily recorded, but most localities lie in protected regions where it may be abundant (e.g. Chobe); therefore, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on habitat associations; protected in various national parks: Kruger (South Africa), Chobe (Botswana), Gorongosa (Mozambique).



Onthophagus vylderi

d'Orbigny, 1913

No synonyms

Global: LC
Endemic: RSA, Botswana, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Sud-Ouest africain allemand: Damara' [inexact: Damaraland, Namibia].

Taxonomy: Accepted Group 20 species; material cited, here, matches original description.

Distribution: Dry to moist savanna on deep Kalahari sands: South Africa, Botswana; also Namibia, but no recent records.

Locality data (mean ± SD, range): Altitude: 1 050 ± 173, 871–1 376 m; annual rainfall: 588 ± 101, 352–659 mm; annual temperature (max. + min. /2): 20.8 ± 1.5, 18.6–22.4°C (N=8).

Habitat: No quantitative assessment; only known from deep sands in open woodland.

Food types: On deep sands in Botswana: sampled only to carrion (chicken livers: 36), not recorded to dung (0: pig, elephant, cattle, sheep) (cited as *Onthophagus* sp. 3); long series from deep sands at Nylsvlei sampled to faeces, meat or banana; limited DBRU collection records from goat carrion and dead millipede.

Temporal activity: Diurnal flight activity during the summer rainy season (Oct. to Feb.).

Ecoregions Botswana: Deep sands in Kalahari Xeric Savanna (AT1309), Zambezian and Mopane Woodlands (AT0725), Zambezian Baikiaea Woodlands (AT0726).

Bioregions South Africa: Deep sand patches in Central Bushveld (SVcb) (Savanna Biome).

Assessment rationale: EOO = 241 110 km^2 (based on available Botswana and South Africa localities); probably a deep sand, carrion specialist, but quantitative data on habitat associations are lacking; food specialisation may be the reason for patchy records; however, widespread range across an area where deep sands are extensive with several localities coinciding with protected areas; therefore, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative ecological data, including further food association records; protected in Chobe National Park (Botswana), Nylsvlei Nature Reserve (South Africa).

Genus *Phalops* Erichson, 1847b

Type species and designation: *Copris ciconia* Fabricius, 1801, by subsequent designation (Shipp 1895c).
Synonyms: = *Coprioides* Gistel, 1857: Type species: *Onthophagus fimbriatus* Klug, 1835, by monotypy.
= *Ephillopus* Reitter, 1892: Type species: *Scarabaeus iphis* Olivier, 1789, by original designation.
Last review: Entire genus reviewed by Barbero et al. (2003); one species transferred from *Onthophagus* Latreille, 1802 (Génier 2013).

The long-established genus, *Phalops* Erichson, 1847b, currently comprises 38 species with distributions in the savannas, upland grasslands and arid areas of the Afrotropical (33), W Oriental (4) and extreme S Palaearctic regions (Arabia: 1). The genus has been divided into six species groups (Barbero et al. 2003).

In South Africa, Botswana and Namibia, *Phalops* is represented by 13 species in five different species groups.

(1) ***iphis* group:** One dry savanna species with a range extending into the E tropics.

(2) ***boschas* group:** Two species with W savanna or E savanna ranges, the latter with a range extending into the E tropics.

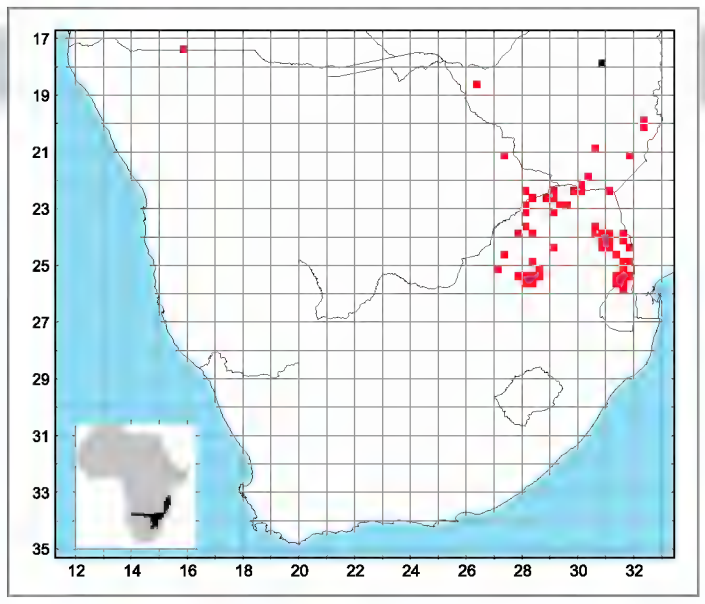
(3) ***prasinus* group:** One species with a dry W savanna range.

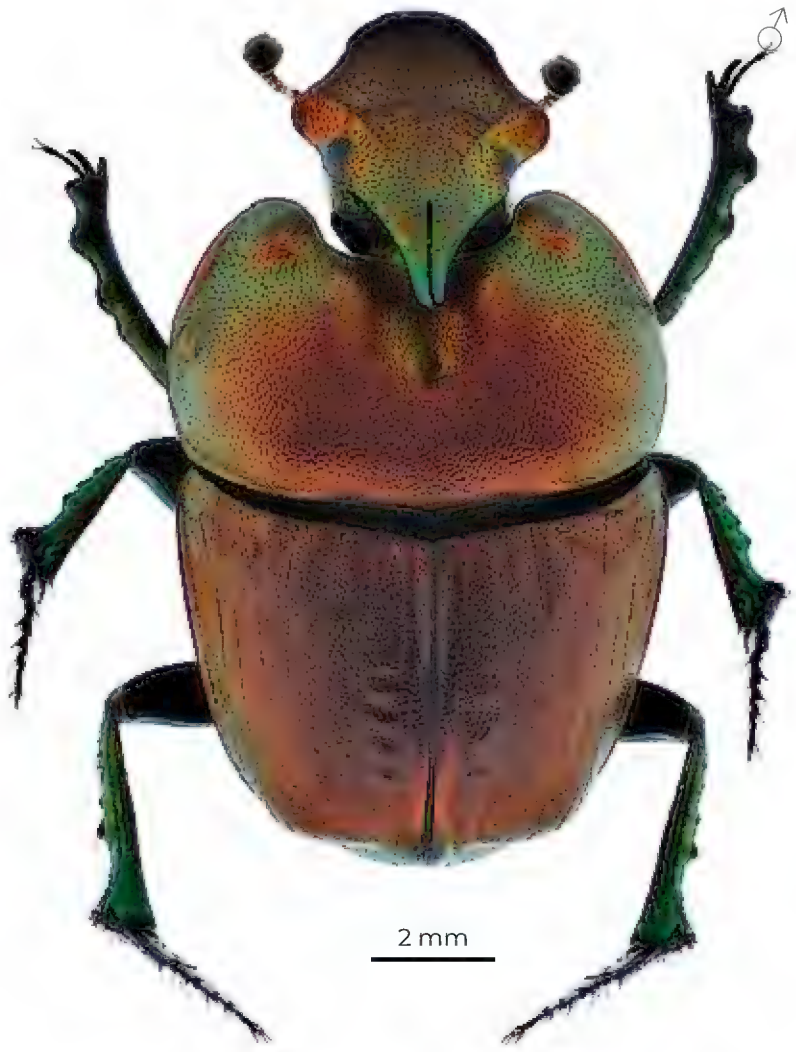
(4) ***divisus* group:** Three species; one with a dry E savanna grassland range extending into the E tropics; the other two closely related and restricted to southern Africa; one with a dry W savanna and arid SW Karoo range; one with an arid W savanna range.

(5) ***fimbriatus* group:** Five species; one with an E savanna range extending into the E tropics; the others all closely related and restricted to southern Africa; one with a savanna, dry W highland grassland and Upper Karoo range; one with an Upper Karoo and dry W savanna range; one with a dry W savanna range; one centred on deep Kalahari sands and outliers.

One recently transferred species, centred on Highveld Grassland and E Upper Karoo of South Africa, has not been assigned to a group.

As most species show widespread distributions with high frequency of occurrence in open vegetation, all but one have been assessed as Least Concern (LC). However, some savanna species show a bias to open woodland, mostly those species with ranges extending into the E tropics. Thus, clearance of trees and shrubs would reduce their population density.





Phalops ardea

(Klug, 1855)

= *Onthophagus* (*Phalops*) *ardea* var. *chloritus* d'Orbigny, 1902

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Onthophagus ardea*: 'Tette und Sena', lectotype: 'Senna...Sinna Tette' [central Mozambique: Sena and Tete]; var. *chloritus*: 'Afrique orientale allemande: Bagamoyo' [Bagamoyo, Tanzania]

Taxonomy: Accepted species of the *iphis* group; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size; iridescent colour variation from cupreous to green to blue.

Distribution: Centred on hot, dry lowland savanna in southern Africa with a recorded distribution extending northwards from dry S central African savanna along the hot, moist E seaboard: NE South Africa, E Botswana, Zimbabwe, N Namibia, SW Angola, Zambia, Malawi, Mozambique, E Tanzania; reports from Kenya and Uganda require validation; black square: surprising locality.

Locality data (mean ± SD, range): Altitude: 662 ± 374, 0–1 751 m; annual rainfall: 618 ± 240, 304–1 748 mm; annual temperature (max. + min. /2): 21.5 ± 1.8, 16.5–25.9°C (N=97).

Habitat: No adequate quantitative assessment; at Leeuwfontein Nature Reserve: bias to finer-grained soils without stones: sand (7), sandy loam (26), stony sandy loam (10); supported by DBRU collection records: sand (6), sandy loam (22), sandy clay loam (6) with bias to open woodland vegetation: grassland/pasture (7), shrubland (1), open woodland (24), forest (1).

Food types: At Phalaborwa: greatest attraction to omnivore dung (pig: 234), frequency less on ruminant and monogastric herbivore dung (cattle: 41; elephant: 17); DBRU collection records reflect commonly sampled dung types: cattle (26), elephant (9), donkey (4), horse (3), also on single rhinoceros, zebra, hyaena and impala droppings.

Temporal activity: Diurnal flight activity, primarily during the summer rainy season (Oct. to Mar.); at Phalaborwa: frequency much greater in hot, dry conditions (243) than in warm cloudy conditions following light rainfall (13), or, in warm sunny conditions soon after heavy rainfall (35).

Ecoregions Namibia, Botswana, Zimbabwe: Angolan Mopane Woodlands (AT0702), Southern African Bushveld (AT0717), Zambezian and Mopane Woodlands (AT0725).

Bioregions South Africa: Central Bushveld (SVcb), Mopane (SVmp), N Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 1 179 470 km^2; AOO may be influenced by soil and vegetation specialisation; across South African range, habitat transformation varies from 0 to 40% (SVmp), 0–58% (SVcb), 2–49% (SVl); nevertheless, widespread in hot, dry, lowland savanna both within and outside of reserves where it is commonly found in the dung of domestic livestock despite a bias to omnivore dung; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by further quantitative data on habitat associations, particularly, effects of woodland clearance; protected in Kruger National Park (South Africa).

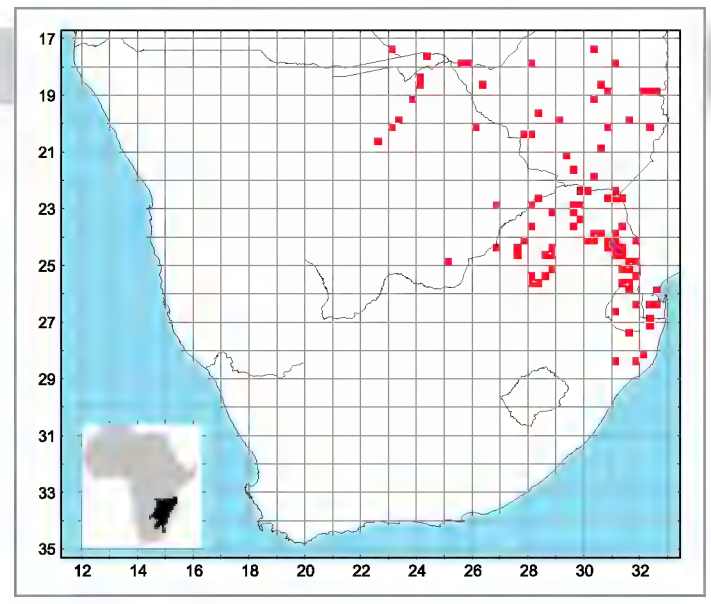
Phalops boschas

(Klug, 1855)

= *Onthophagus* (*Phalops*) *boschas* var. *chloronotus* d'Orbigny, 1902

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: As *Onthophagus boschas*: 'Sena', lectotype: 'Sinna' [Sena, central Mozambique]; var. *chloronotus*: 'Nyassa' [Mozambique].

Taxonomy: Accepted species of the *boschas* group; little colour variation; mostly dark, sometimes with green sheen; limited sexual dimorphism (head, prothoracic disc), characters vary in prominence with body size.

Distribution: Centred on hot, fairly dry, southern African savanna with a recorded distribution extending northwards from S central African savanna along the hot, moist E seaboard: NE South Africa, NE Botswana, Zimbabwe, NE Namibia, SE Angola, Zambia, Malawi, Mozambique, S Democratic Republic of the Congo (DRC), E Tanzania; report from Kenya requires validation.

Locality data (mean ± SD, range): Altitude: 724 ± 381, 0–1 503 m; annual rainfall: 630 ± 136, 306–1 151 mm; annual temperature (max. + min. /2): 21.1 ± 1.8, 17.1–25.7°C (N=130).

Habitat: No adequate quantitative assessment; at Leeuwfontein Nature Reserve: biased to finer-grained soils without stones: sand (8), sandy loam (13), stony sandy loam (7); supported by DBRU collection records: sand (12), sandy loam (27), sandy clay loam (8), clay (1) with bias to woodland vegetation: grassland/pasture (10), shrubland (2), open woodland (30).

Food types: At Phalaborwa: greatest attraction to omnivore dung (pig: 173), frequency lower on ruminant and monogastric herbivore dung (cattle: 19; elephant: 9); DBRU collection records reflect commonly sampled dung types: cattle (41), elephant (8), rhinoceros (4), also on single baboon, donkey, warthog, wildebeest and waterbuck droppings.

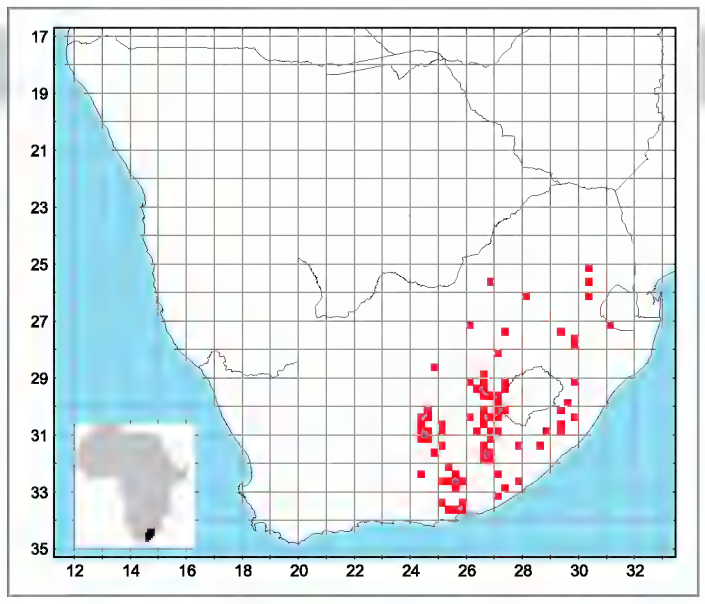
Temporal activity: Diurnal flight activity, primarily during the summer rainy season (Oct. to Apr.); at Phalaborwa: frequency much greater in hot, dry conditions (176) than in warm cloudy conditions following light rainfall (9), or in warm sunny conditions soon after heavy rainfall (16).

Ecoregions Namibia, Botswana, Zimbabwe, Mozambique: E Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian Baikiaea Woodlands (AT0726), Zambezian and Mopane Woodlands (AT0725), Southern African Bushveld (AT0717), Southern Miombo Woodlands (AT0719), Maputaland Coastal Forest Mosaic (AT0119).

Bioregions South Africa: Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 2 069 530 km^2; centred in hot lowland savanna both within and outside of reserves where it is found sporadically in dung of domestic livestock, perhaps reflecting the measured bias to omnivore dung; across South African range, habitat transformation varies from 0 to 40% (SVmp), 0–58% (SVcb), 2–49% (SVl); however, very widespread, so assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by further quantitative data on habitat associations, particularly, effects of woodland clearance; protected in Kruger National Park (South Africa).



Phalops bubalus

(Harold, 1867c)

No synonyms

Global: LC (see IUCN Red List as *Onthophagus* – LC)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Onthophagus bubalus*: 'Cap der guten Hoffnung' [Cape of Good Hope, South Africa].

Taxonomy: Accepted species; not assigned to a species group; no formally described synonyms although Harold cites *O. bubalus* Klug *in litt.* and *O. varipennis* Dejean (catalogue) as synonyms; recently transferred from *Onthophagus* Group 13, but horn of males differs to those of other *Phalops*; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.

Distribution: Centred on the South African Highveld and cooler coastal parts of the Eastern Cape lying within the summer rainfall region; possibly more abundant in drier areas.

Locality data (mean ± SD, range): Altitude: 1 256 ± 417, 145–2 199 m; annual rainfall: 527 ± 163, 301–843 mm; annual temperature (max. + min. /2): 15.6 ± 1.4, 11.2–18.7°C (N=108).

Habitat: No adequate quantitative assessment; on the KwaZulu-Natal escarpment (29–30°S): limited numbers recorded in grassland on sandy clay loam only at 1 500 m, not at lower (500 m, 1 000 m) nor higher altitudes (1 900 m, 2 400 m, 2 800 m); at the SW edge of the range in E Upper Nama Karoo: recorded at an average of three per sample at 36 study sites on nine farms; DBRU collection records on sand (12), sandy loam (23), sandy clay loam (33), clay (5) in grassland/pasture (35), scrub/shrubland (5), open woodland (2).

Food types: No quantitative assessment; DBRU collection records from cattle (78) and buffalo (1) dung.

Temporal activity: Diel flight periodicity unknown; active primarily during the summer rainy season (Oct. to May).

Bioregions South Africa: Centred on Dry Highveld Grassland (Gh), Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs) (Grassland Biome); Albany Thicket Biome (AT); Eastern Upper Karoo (NKu 4) (Nama Karoo Biome).

Assessment rationale: EOO = 355 495 km^2; primarily distributed in farmland across the grasslands of the South African Highveld where it readily colonises cattle dung; range extensively transformed by cultivation and pasture improvement (1–63%, Gh; 1–69%, Gm; 2–50%, Gs; 2% NKu); however, widespread occurrence; therefore, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, particularly, effects of habitat transformation such as pasture improvement in natural grassland; protected in Addo Elephant National Park.

Phalops dregei

(Harold, 1867c)

= *Phalops rufosignatus* van Lansberge, 1885a (*pars*)
= *Phalops adspersipennis* Boheman, 1857, *sensu* Péringuey, 1901 (*pars*)
= *Phalops congenitus* Péringuey, 1901

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Onthophagus dregei*: 'Cap der guten Hoffnung', lectotype: 'Pr. b. sp.' [Cape of Good Hope, South Africa]; *P. rufosignatus* (*pars*): 'l'Afrique méridionale' [southern Africa]; *P. adspersipennis* (*pars*): 'Ovampoland (Omrramba), ? Southern Rhodesia' [Namibia, Zimbabwe]; *P. congenitus*: 'Transvaal (Potchefstroom, Lydenburg), British Bechuanaland (Palapye), Southern Rhodesia (Buluwayo)' [South Africa, Botswana, Zimbabwe].

Taxonomy: Accepted species in the *fimbriatus* group, but see also taxonomic notes under *P. rufosignatus* van Lansberge; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size; colour variation from iridescent cupreous in warmer NE lowland range to black head and thorax with brown elytra in higher SW Highveld range.

Distribution: Dry savanna in the NE to dry grassland or shrubland in the SW; primarily found in South Africa with scattered records from savannas of Zimbabwe, Botswana and Namibia.

Locality data (mean ± SD, range): Altitude: 1 102 ± 341, 106–1 860 m; annual rainfall: 431 ± 171, 195–769 mm; annual temperature (max. + min. /2): 17.9 ± 2.4, 13.2–23.2°C (N=178).

Habitat: No adequate quantitative assessment; in Gauteng bushveld: sand (5), sandy clay loam (8) in grassland (8), open woodland (5), shaded thickets (0); in open woodland at Leeuwfontein Nature Reserve: clear bias to stony finer-grained soils: sand (68), sandy loam (109), stony sandy loam (321); DBRU collection records: sand (16), sandy loam (24), sandy clay loam (11) in grassland/pasture (18), scrub/shrubland (12), open woodland (10).

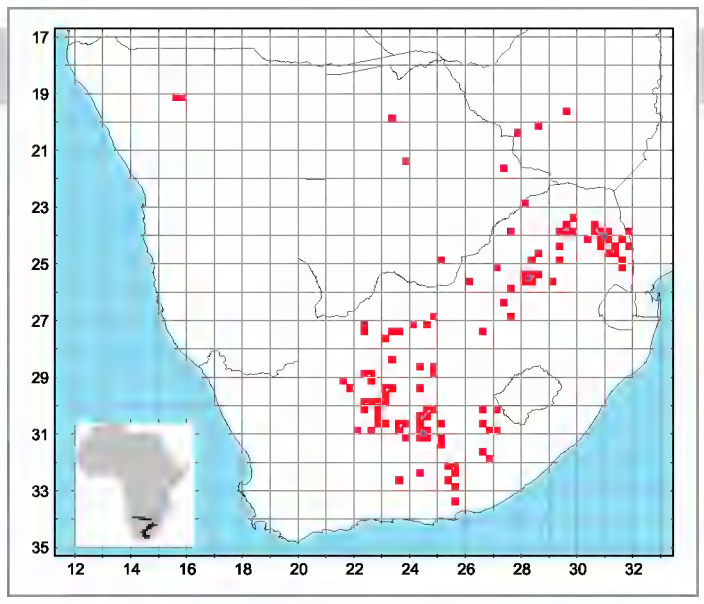
Food types: At Phalaborwa: greatest attraction to omnivore dung (pig: 140), frequency lower on ruminant and monogastric herbivore dung (cattle: 43; elephant: 27); DBRU collection records reflect commonly sampled dung types: cattle (43), zebra (2), horse (1).

Temporal activity: Diurnal flight activity, during the summer rainy season (Oct. to Apr.); at Phalaborwa: frequency much greater in hot, dry conditions (141) than in warm cloudy conditions following light rainfall (20), or in warm sunny conditions soon after heavy rainfall (26).

Ecoregions Namibia, Botswana, Zimbabwe: Angolan Mopane Woodlands (AT0702), Kalahari Acacia-Baikiaea Woodlands (AT0709), Southern African Bushveld (AT0717), S Zambezian and Mopane Woodlands (AT0725).

Bioregions South Africa: Central Lowveld (SVl), Central Bushveld (SVcb), Eastern Kalahari Bushveld (SVk) (Savanna Biome); N and S Dry Highveld Grassland (Gh) (Grassland Biome); N Upper Karoo (NKu) (Nama Karoo Biome); Albany Thicket Biome (AT); margins of five other bioregions.

Assessment rationale: EOO = 500 430 km^2; associated with drier climate in warm savanna, grassland and Karoo; widely recorded in dung of domestic livestock in farmland despite measured bias to omnivore dung;



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Phalops dregei (continued)

SW part of range in Karoo little transformed; greater transformation to NE in SVcb (0–58%) and SVl (2–49%); however, widespread and little threatened over much of range; therefore, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by further quantitative data on soil and vegetation associations; protected in various national parks and nature reserves including Kruger, Telperion (South Africa), Etosha (Namibia).

Phalops flavocinctus

(Klug, 1855)

= *Onthophagus praeustus* Fahraeus, 1857
= *Onthophagus* (*Phalops*) *flavocinctus* var. *nigrostriatus* d'Orbigny, 1902

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Onthophagus flavocinctus*: 'Sena' [Sena, central Mozambique], lectotype: 'Port Natal Sinna' [Unclear: Durban and Sena?]; *O. praeustus*: 'prope fluvium Limpopo' [near Limpopo River, southern Africa]; var. *nigrostriatus*: 'Transvaal' [South Africa].

Taxonomy: Accepted species in the *divisus* group; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size; dull, irridescent, colour variation from cupreous to green to blue.

Distribution: Widespread in open savanna on finer-grained soils along the SE seaboard of Africa: South Africa, Botswana, Zimbabwe, Zambia, Malawi, Mozambique, E Tanzania.

Locality data (mean ± SD, range): Altitude: 716 ± 481, 0–1 652 m; annual rainfall: 677 ± 147, 304–1 191 mm; annual temperature (max. + min. /2): 20.6 ± 2.3, 14.3–26.1°C (N=156).

Habitat: In Gauteng bushveld: extreme bias to sandy clay loam (20) compared to sand (0) in grassland (16) rather than open woodland (4), shaded thicket (0); in uMkhuze Game Reserve: similar bias to finer-grained soils: sand (0.4), sand over clay (3.3), sandy clay loam (9.4), clay (5.3) in unshaded (158) rather than shaded conditions (24); partly supported by DBRU collection records: sand (7), sandy loam (21), sandy clay loam (21), clay (6) in pasture/grassland (15), shrubland (10), open woodland (19), forest/thicket (3).

Food types: At Phalaborwa: greatest attraction to omnivore dung (pig: 60), frequency less on ruminant and monogastric herbivore dung (cattle: 6; elephant: 7); DBRU collection records reflect commonly sampled dung types: cattle (41), buffalo (3), wildebeest (3), elephant (13), rhinoceros (6), horse (2), also on single zebra, donkey, warthog, baboon and impala droppings.

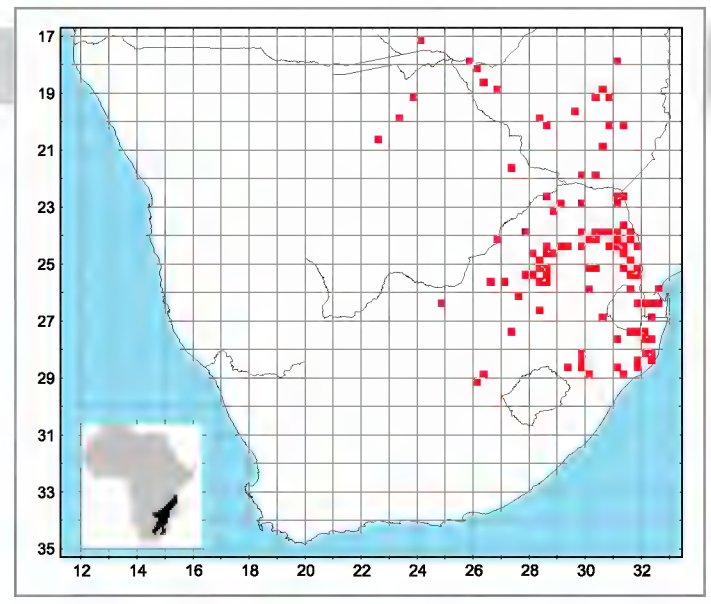
Temporal activity: Diurnal flight activity primarily during the summer rainy season (Oct. to Mar.); at Phalaborwa: frequency much greater in hot, dry conditions (58) than in warm cloudy conditions following light rainfall (2), or, in warm sunny conditions soon after heavy rainfall (13).

Ecoregions Botswana, Zimbabwe, Mozambique: E Kalahari Acacia-Baikiaea Woodlands (AT0709), Southern African Bushveld (AT0717), Zambezian and Mopane Woodlands (AT0725), Southern Miombo Woodlands (AT0719), Maputaland Coastal Forest Mosaic (AT0119).

Bioregions South Africa: Centred on Central Bushveld (SVcb), Lowveld (SVl), Mopane (SVmp) (Savanna Biome); sporadically in warmer N parts, Dry Highveld Grassland (Gh) and Sub-Escarpment Grassland (Gs) (Grassland Biome); margins of four other bioregions.

Assessment rationale: EOO = 1 564 855 km^2; AOO would be smaller, restricted by soil and vegetation specialisation; however, habitat transformation through clearance of woodland in main South African part of range (SVcb: 0–58%; SVl: 2–49%) may not be a great threat owing to grassland habitat bias; furthermore, clearly widespread, therefore, assessed as Least Concern (LC).

Conservation measures: None recommended; widespread in more open vegetation on finer-grained soils and well protected in reserves, including Kruger National Park and uMkhuze Game Reserve (South Africa).



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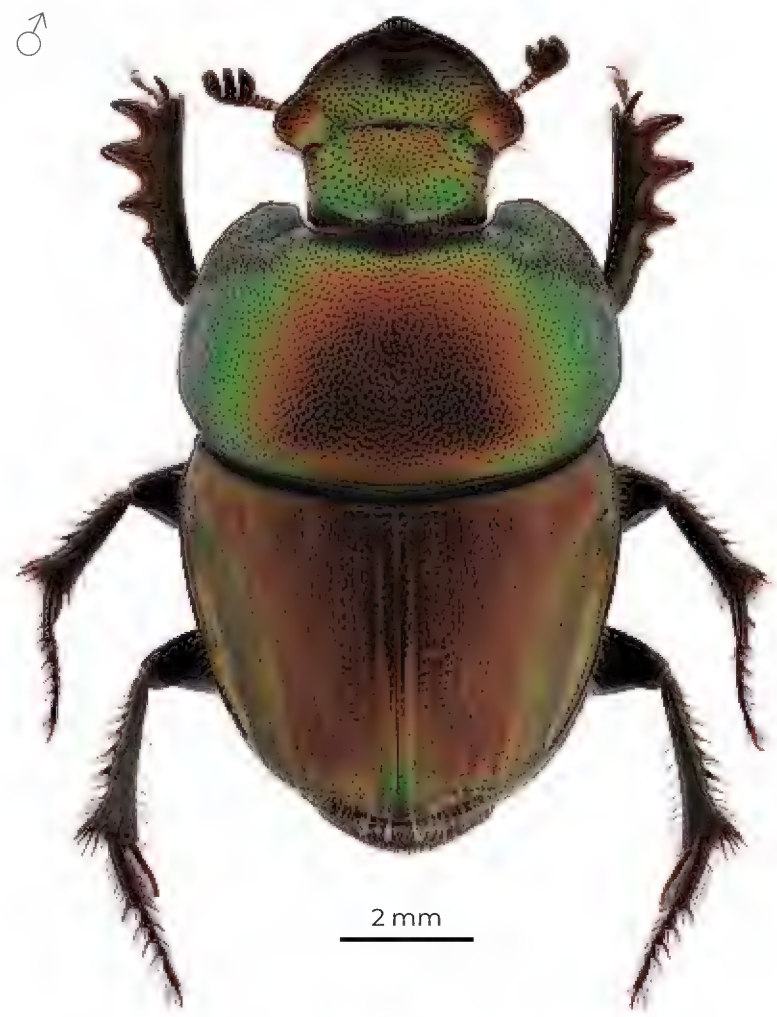

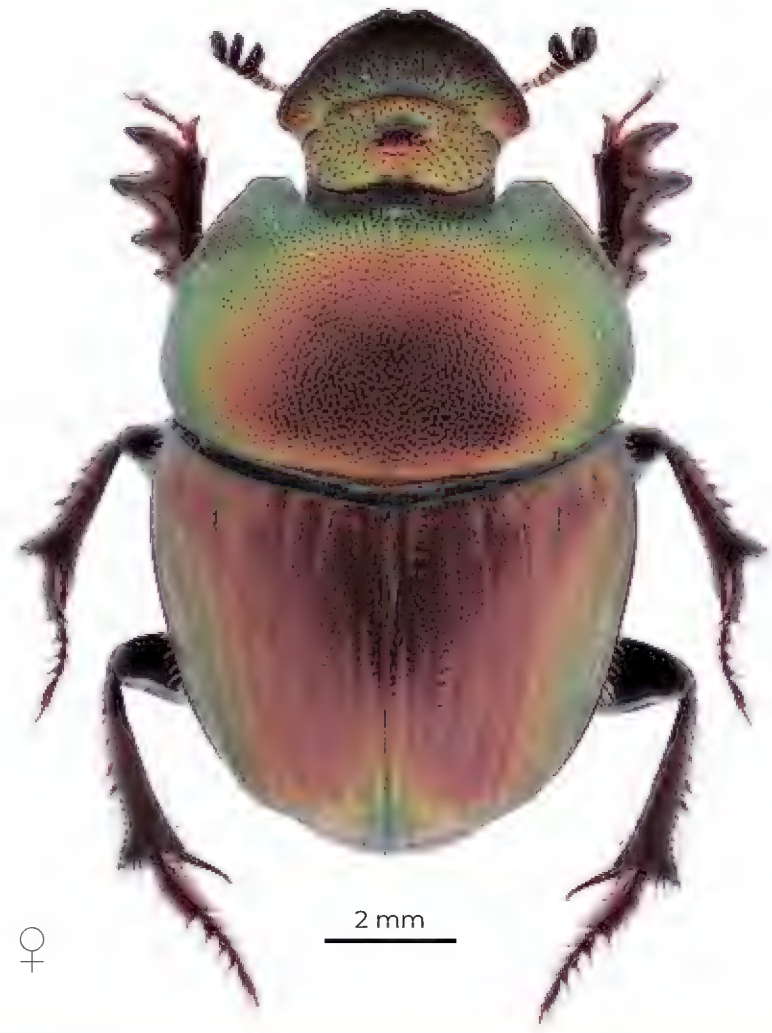

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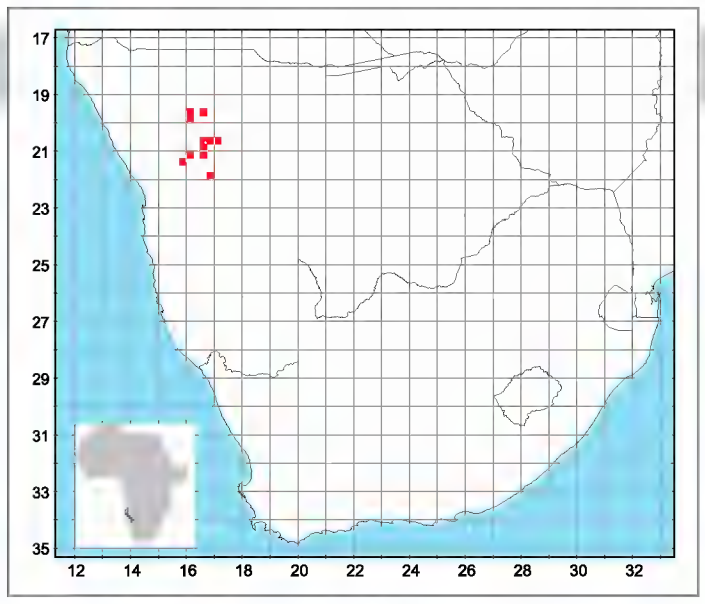


Phalops pauliani

Barbero, Palestrini & Roggero, 2003

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Okosongomingo l49 Otjiwarongo SE 20l7 Ca' [Namibia].

Taxonomy: Accepted species in the *fimbriatus* group; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size; all known individuals iridescent green.

Distribution: Centred on dry upland savanna of N central Namibia with one inexact record from Alto Cubal, Benguela Province, SW Angola.

Locality data (mean ± SD, range): Altitude: 1 437 ± 122, 1 214–1 577 m; annual rainfall: 400 ± 57, 296–480 mm; annual temperature (max. + min. /2): 19.9 ± 1.0, 16.6–21.8°C (N=11).

Habitat: No quantitative assessment; DBRU collection records mainly on finer-grained soils: sand (1), sandy loam (4), clay (1), in woody vegetation: shrubland (1), open woodland (5).

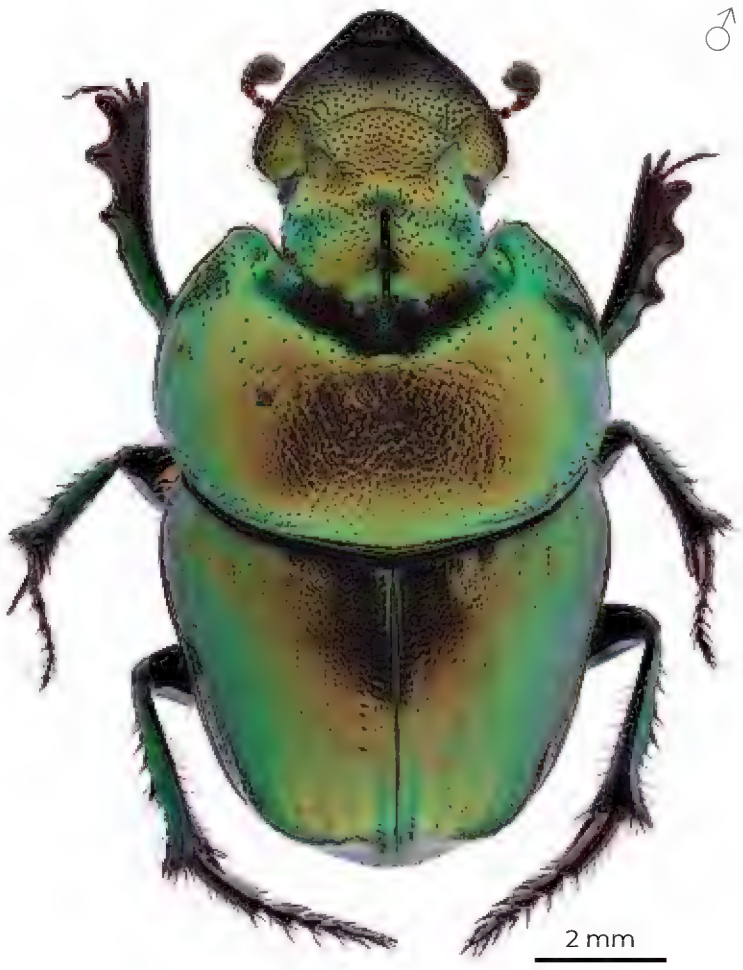
Food types: No quantitative assessment; DBRU collection records on cattle (5) and donkey (1) dung.

Temporal activity: Diurnal flight activity; recorded primarily in the late summer rainy season (Dec. to May).

Ecoregions Namibia: NW Kalahari Xeric Savanna (AT1309), Angolan Mopane Woodlands (AT0702).

Assessment rationale: EOO = 66 480 km^2 (estimated); recently described and known primarily from farm rangeland in open N Namibian savanna woodland; one further record suggests a wider range extending into Angola; recorded from dung of farm livestock and, apparently, not threatened at present; therefore, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by a quantitative survey to determine its full EOO and ecological associations, particularly if it would be influenced by woodland clearance; not currently known to be protected within any reserve.



Phalops plancus

(Erichson, 1843)

= *Onthophagus* (*Phalops*) *densegranosus* d'Orbigny, 1908

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Onthophagus plancus*: 'Angola', lectotype: 'Angola'; *O.* (*P.*) *densegranosus*: 'Great Namaqualand' [SW to W Namibia].

Taxonomy: Accepted iridescent cupreous species in the *divisus* group; minor sexual dimorphism (head).

Distribution: Centred in open arid lowland savanna bordering the Namib and Kaokoveld Deserts in W to NW Namibia and SW Angola.

Locality data (mean ± SD, range): Altitude: 885 ± 336, 283–1 458 m; annual rainfall: 232 ± 88, 44–375 mm; annual temperature (max. + min. /2): 17.0 ± 1.2, 14.5–18.8°C (N=14).

Habitat: No quantitative assessment; DBRU collection records entirely on sand (4) in scrub (2), shrubland (1) or open woodland (1).

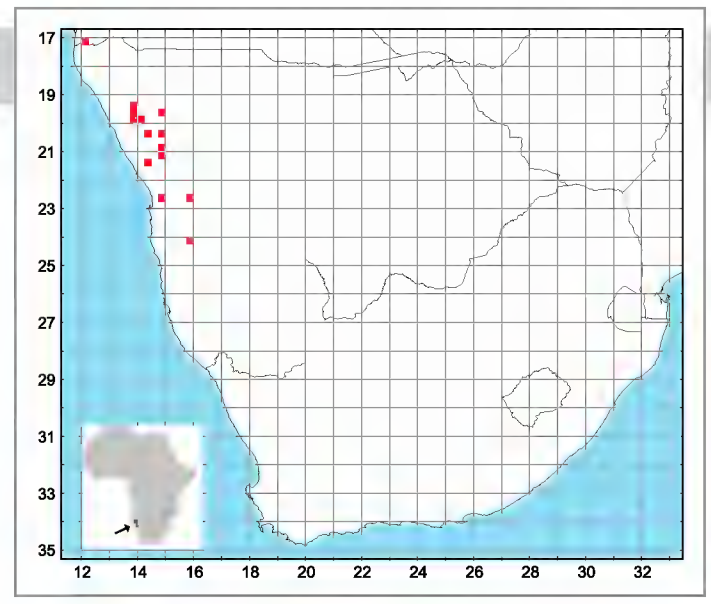
Food types: No quantitative assessment; DBRU collection records on cattle (3) or donkey (1) dung.

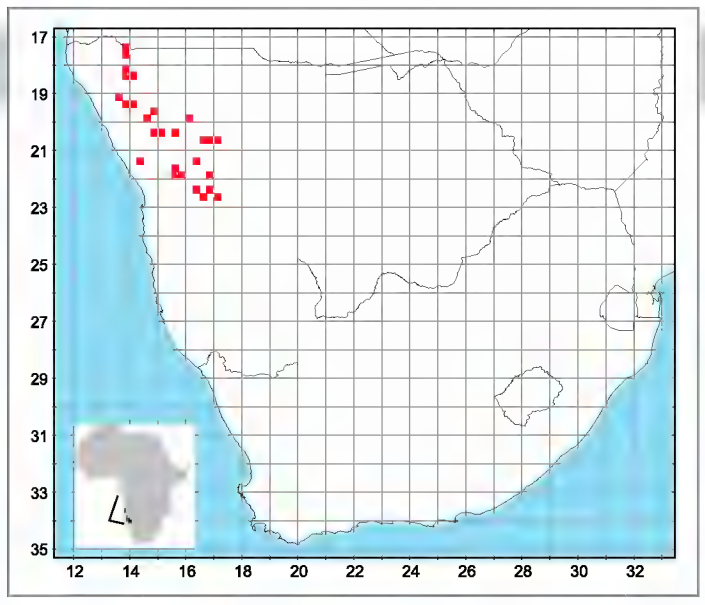
Temporal activity: Diurnal flight activity during the late summer rainy season (Feb. to May).

Ecoregions Namibia: Centred on Namibian Savanna Woodlands (AT1316), also, margins of Namib Desert (AT1315).

Assessment rationale: EOO = 39 635 km²; AOO may be restricted by soil specialisation; found in little-transformed, arid savanna used primarily for grazing of livestock; therefore, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; not currently known from any national park although widely protected in community conservation areas.





Phalops prasinus

(Erichson, 1843)

= *Onthophagus adspersipennis* Boheman, 1860
= *Onthophagus* (*Phalops*) *prasinus* var. *aeraneus* d'Orbigny, 1902

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Onthophagus prasinus*: 'Angola', lectotype: 'Angola'; *O. adspersipennis*: 'regione fluvii Svakop' [Swakop River region, Namibia]; var. *aeraneus*: Not stated.

Taxonomy: Accepted species in the *prasinus* group; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.

Distribution: Centred on dry savanna in N Namibia with a dry to moderately moist savanna range continuing along a narrow W coastal belt in Angola to Democratic Republic of the Congo (DRC); record from wet tropical Gabon seems doubtful.

Locality data (mean ± SD, range): Altitude: 1 203 ± 313, 536–1 730 m; annual rainfall: 324 ± 87, 171–507 mm; annual temperature (max. + min. /2): 18.5 ± 1.3, 16.3–20.7°C (N=32).

Habitat: No quantitative assessment; DBRU collection records suggest a bias to coarser-grained soils: sand (6), sandy loam (4), clay (1), in woody vegetation: scrub (1), shrubland (5), open woodland (6).

Food types: No quantitative assessment; DBRU collection records from cattle (8), horse (2) and donkey (2) dung.

Temporal activity: Diurnal flight activity during the late summer rainy season (Dec. to Apr.).

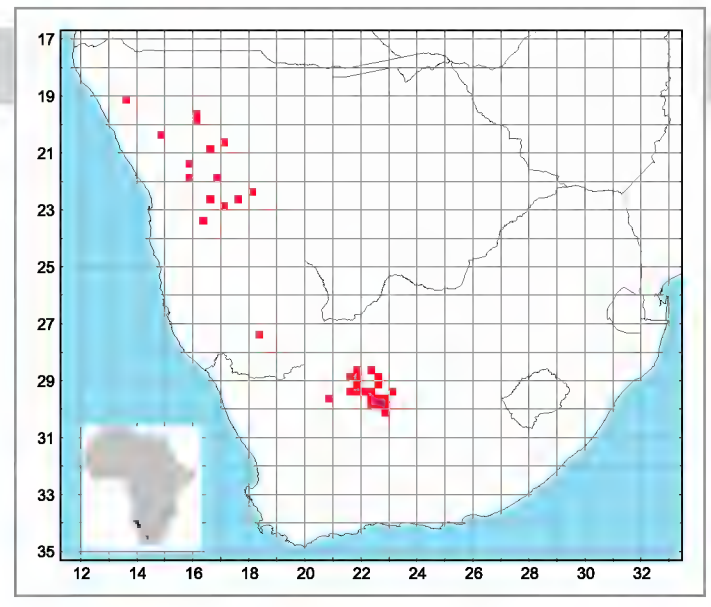
Ecoregions Namibia: Centred on NW Kalahari Xeric Savanna (AT1309), N Namibian Savanna Woodlands (AT1316); marginal in Angolan Mopane Woodlands (AT0702), Namib Desert (AT1315).

Assessment rationale: EOO = 115 340 km^2; widespread on sandy soils in N Namibian savanna woodland; EOO primarily coincides with farm rangeland where it has been recorded on the dung of farm livestock; probably not currently threatened by habitat transformation, therefore, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; protected in Etosha National Park (Namibia).

Phalops pyroides

(d'Orbigny, 1908)



No synonyms

Global: LC
Endemic: RSA, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Onthophagus* (*Phalops*) *pyroides*: 'Damaraland (Okahandja; Windhoek)', lectotype: 'Okahandja' [Namibia].

Taxonomy: Accepted iridescent cupreous species in the *fimbriatus* group; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.

Distribution: Centred on dry N Namibian savanna woodland and arid Northern Cape Karoo, South Africa; apparent disjunction may be a collecting artefact.

Locality data (mean ± SD, range): Altitude: 1 133 ± 224, 783–1 928 m; annual rainfall: 242 ± 66, 133–439 mm; annual temperature (max. + min. /2): 18.7 ± 0.9, 15.8–22.8°C (N=61).

Habitat: No adequate quantitative data; in Northern Cape: similar abundance on sand (1.01) and sandy loam (0.98) in grassland, scrub or shrubland; DBRU collection records from N Namibia on sand (1), sandy loam (3), sandy clay loam (1), clay (1) in scrub (1), shrubland (1), open woodland (4).

Food types: No quantitative data; DBRU collection records on cattle (5) and donkey (1) dung.

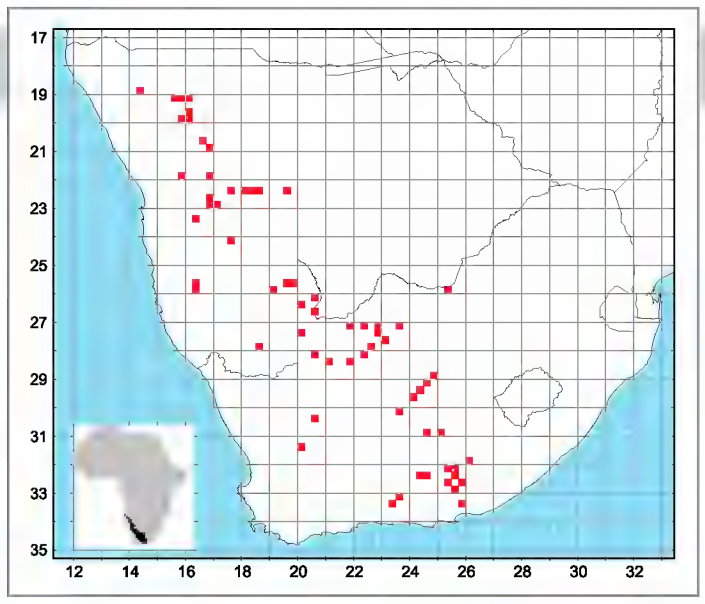
Temporal activity: Diurnal flight activity in the late summer rainy season (Jan. to Apr.).

Ecoregions Namibia: Nama Karoo (AT1314), NW Kalahari Xeric Savanna (AT1309), Namibian Savanna Woodlands (AT1316), S Angolan Mopane Woodlands (AT0702).

Bioregions South Africa: NE Bushmanland (NKb) (Nama Karoo Biome) and incorporated outlier patches of Kalahari Duneveld (SVkd) (Savanna Biome).

Assessment rationale: EOO = 122 540 km^2; observed habitat association varies from dry woody savanna (N Namibia) to arid grass, scrub, and shrubland Karoo of NE Bushmanland (W Griqualand, South Africa); habitat transformation low as land use is dominated by grazing of domestic livestock to whose dung it is readily attracted; therefore, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by a survey to determine if its distribution is disjunct or continuous; owing to the degree of variability in observations, a quantitative study of ecological associations would also be useful in both the S and the N; not known to occur in any protected area.



Phalops rufosignatus

van Lansberge, 1885a

= *Phalops euplynes* Bates, 1888
= *Phalops adspersipennis* Boheman, 1857, *sensu* Péringuey, 1901 (*pars*)
= *Onthophagus* (*Phalops*) *lansbergei* d'Orbigny, 1902 (*pars*)

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *P. rufosignatus* (*pars*): 'l'Afrique méridionale' [southern Africa]; *P. euplynes*: 'Damara Land' [Namibia]; *P. adspersipennis sensu* Péringuey *(pars)* 'Cape Colony (Calvinia, Bushmanland, Namaqualand)' [South Africa]; *O.* (*P.*) *lansbergei* (*pars*): invalidated *nom nov.* for *P. rufosignatus*.

Taxonomy: Accepted species in the *divisus* group, but designated type series comprises one male *P. dregei* Harold, 1867, and one female *P. rufosignatus*; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.

Distribution: Centred on the arid late summer rainfall region in SW Africa: South Africa, Namibia, SW Angola, extreme SW Botswana; Tanzania record requires further validation.

Locality data (mean ± SD, range): Altitude: 1 161 ± 348, 0–1 928 m; annual rainfall: 311 ± 101, 59–486 mm; annual temperature (max. + min. /2): 18.6 ± 2.2, 13.3–22.5°C (N=76).

Habitat: No quantitative assessment; DBRU collection records from sand (31), sandy loam (17), sandy clay loam (23), clay (1) in grassland/pasture (14), scrub (17), shrubland (16), open woodland (15).

Food types: In Botswana: bias to dung of omnivores (pig: 101), pellet-dropping ruminant and monogastric herbivores (sheep: 74; elephant: 35) rather than pad-dropping ruminant herbivores (cattle: 9); DBRU collection records reflect commonly sampled dung types: cattle (57), buffalo (1), wildebeest (2), elephant (2), zebra (3), horse (3), donkey (4).

Temporal activity: Diurnal flight activity, primarily, during the late summer rainy season (Dec. to May) with few records in July, Oct. and Nov.

Ecoregions Namibia: Nama Karoo (AT1314), W Kalahari Xeric Savanna (AT1309), Namibian Savanna Woodlands (AT1316), S Angolan Mopane Woodlands (AT0702).

Bioregions South Africa: Upper Karoo (NKu), Bushmanland (NKb) (Nama Karoo Biome), Eastern Kalahari Bushveld (SVk), Kalahari Duneveld (SVkd) (Savanna Biome); also Albany Thicket Biome (AT).

Assessment rationale: EOO = 591 895 km^2; widespread across various soil and vegetation types in a little-transformed region used primarily for the grazing of domestic livestock to whose dung it is readily attracted despite a measured bias to omnivore dung; therefore, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on habitat associations; protected in Kgalagadi Transfrontier Park (South Africa, Botswana), Etosha National Park (Namibia).

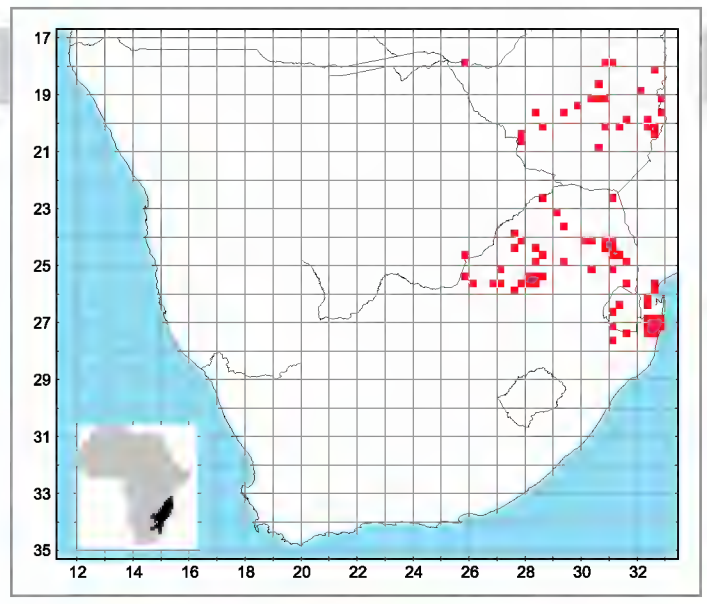
Phalops smaragdinus

(Harold, 1875)

= *Onthophagus tarsatus* Péringuey, 1888
= *Onthophagus* (*Phalops*) *smaragdinus* var. *coerulosus* d'Orbigny, 1902
= *Onthophagus* (*Phalops*) *smaragdinus* var. *cuprinus* d'Orbigny, 1902
= *Onthophagus smaragdinus n. f. idiomelas* Kuntzen, 1913

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: As *Onthophagus smaragdinus*: 'Abyssinia australis' [?southern Ethiopia], lectotype: 'Holub' [possibly refers to the 19th century collector, E. Holub, who travelled South and central Africa]; *O. tarsatus*: 'Rustenburg and Potchefstroom, Transvaal' [North-West Province, South Africa]; var. *coerulosus*: 'Transvaal' [South Africa]; var. *cuprinus*: 'Zanzibar' [Tanzania]; *n. f. idiomelas*: Not stated.

Taxonomy: Accepted species in the *fimbriatus* group, but cited NE African occurrence of original type, compared to SE African occurrence of lectotype and varieties, suggests re-evaluation might be warranted, particularly, in comparison with the close East African relative, *P. lamininfrons* Fairmaire, 1882, described from Zanzibar; sexually dimorphic (head, prothoraccic disc), characters vary in prominence with body size; iridescent colour variation from cupreous to green to blue.

Distribution: Validated distribution centre in SE Africa: South Africa, E Botswana, Zimbabwe, Malawi, Mozambique; also reported from Zambia, SE Tanzania; records from Namibia, N Tanzania, Uganda, and original type locality of Ethiopia (cited as Abyssinia australis) require further validation.

Locality data (mean ± SD, range): Altitude: 825 ± 473, 0–1 785 m; annual rainfall: 731 ± 178, 304–1 259 mm; annual temperature (max. + min. /2): 20.4 ± 2.1, 14.8–25.4°C (N=107).

Habitat: In Gauteng bushveld: extreme bias to sand (96) rather than sandy clay loam (0) with very strong bias to open woodland (86) rather than grassland (9) or shaded thickets (1); weakly supported by DBRU collection records on sand (14), sandy loam (16), sandy clay loam (10) in pasture/grassland (13), open shrub/woodland (17), thickets (1).

Food types: No adequate quantitative assessment; at Phalaborwa: only recorded to pig dung (8), none to cattle or elephant dung; DBRU collection records from dung of cattle (42), elephant (1), donkey (1), human/cattle mix (1).

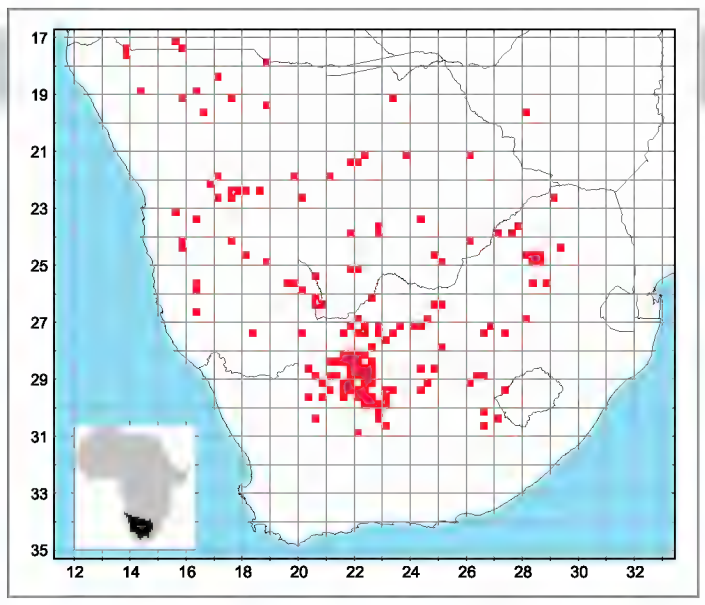
Temporal activity: Diurnal flight activity, primarily during the summer rainy season (Oct. to Apr.).

Ecoregions Botswana, Zimbabwe, Mozambique: E Kalahari Acacia-Baikiaea Woodlands (AT0709), Southern African Bushveld (AT0717), Zambezian and Mopane Woodlands (AT0725), Southern Miombo Woodlands (AT0719), Maputaland Coastal Forest Mosaic (AT0119), margins of two other ecoregions.

Bioregions South Africa: Centred on Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome); N Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 1 479 555 km²; AOO possibly reduced by soil and vegetation bias; in South Africa, habitat transformation across its range varies from 0 to 58% (SVcb) and 2–49% (SVl), with clearance of woodland possibly detrimental to population density; currently assessed as Least Concern (LC) on basis of high frequency of records across a large EOO.

Conservation measures: Assessment of conservation status would be improved by further quantitative ecological data to support soil, vegetation and dung type specialisation; protected in Tswaing Nature Reserve, Kruger National Park (South Africa), Lake Mutirikwe Game Reserve (Zimbabwe).



Phalops wittei

(Harold, 1867c)

= *Onthophagus boschimanus* Péringuey, 1888
= *Onthophagus adspersipennis* Boheman, 1857, *sensu* Péringuey, 1901 (*pars*)
= *Onthophagus* (*Phalops*) *rufatus* d'Orbigny, 1902

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Onthophagus wittei*: 'innere Südafrika, Owampo', lectotype: 'Owampo' [South African interior; Ovamboland, Namibia]; *O. boschimanus*: 'Bushmanland' [Northern Cape, South Africa]; *O. adspersipennis* (*pars*): 'Ovampoland (Omrramba)' [Omuramba, Namibia]; *O.* (*P.*) *rufatus*: 'Angola: Benguella' [Benguela].

Taxonomy: Accepted species in the *fimbriatus* group with black head and prothoracic disc with brown elytra; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size; synonymy of *Phalops rufatus* is based on the single female type specimen comprising parts of two different species (Barbero et al. 2003), however, this decision may require re-examination, as material from arid NW Namibia appears to differ a little from *P. wittei*.

Distribution: Centred on deep sands in drier climates of southern Africa: N central South Africa, Namibia, Botswana, SW Zimbabwe, SW Angola.

Locality data (mean ± SD, range): Altitude: 1 102 ± 217, 0–2 199 m; annual rainfall: 300 ± 136, 59–741 mm; annual temperature (max. + min. /2): 19.2 ± 1.6, 11.2–23.1°C (N=254).

Habitat: In Gauteng bushveld: extreme bias to sand (41) as opposed to sandy clay loam (0) and grassland (39) as opposed to open woodland (2) or shaded thickets (0); largely supported by DBRU collection records on sand (58), sandy loam (6), sandy clay loam (4) in grassland/pasture (18), scrub (13), shrubland (20), open woodland (12).

Food types: In Botswana: bias to dung of omnivores (pig: 190), pellet-dropping ruminant and monogastric herbivores (sheep: 103; elephant: 77) rather than pad-dropping ruminant herbivores (cattle: 8); DBRU collection records mostly reflect commonly sampled dung types: baboon (1), cattle (59), wildebeest (1), elephant (1), horse (2), donkey (2).

Temporal activity: Diurnal flight activity, primarily during the mid- and late summer rainy seasons (Oct. to Apr./May).

Ecoregions Namibia, Botswana, Zimbabwe: Widespread across deep sands of Namibian Savanna Woodlands (AT1316), Kalahari Xeric Savanna (AT1309), Kalahari Acacia-Baikiaea Woodlands (AT0709), S Angolan Mopane Woodlands (AT0702), margins of four adjoining ecoregions.

Bioregions South Africa: Deep sands of Bushmanland (NKb) (Nama Karoo Biome); Dry Highveld Grassland (Gh) (Grassland Biome); Kalahari Duneveld (SVkd), Eastern Kalahari Bushveld (SVk), Central Bushveld (SVcb) (Savanna Biome); margins of three other bioregions.

Assessment rationale: EOO = 1 562 330 km^2; AOO reduced by soil specialisation and bias to open vegetation, but much of range comprises continuous, little-transformed, sparsely vegetated, deep Kalahari sands used primarily for grazing of domestic livestock to which *P. wittei* is widely attracted despite a recorded bias to omnivore dung; therefore, assessed as Least Concern (LC).

Conservation measures: None recommended; protected in the private Tswalu Kalahari Reserve, Kgalagadi Transfrontier Park (South Africa, Botswana).

Phalops zuninoi

Barbero, Palestrini & Roggero, 2003

No synonyms

Global: DD

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Bicuari N. P. Angola (Nr Campo)' [near camp in Bicuar National Park, Angola].

Taxonomy: Accepted species in the *boschas* group; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.

Distribution: Recently described from moist climate at S edge of Bié Plateau and adjoining deep sands, S Angola; also recorded on deep sands of Ovamboland floodplain, N Namibia, and Liuwa floodplain, SW Zambia.

Locality data (mean ± SD, range): Altitude: 1 158 ± 70, 1 109–1 207 m; annual rainfall: 674 ± 197, 534–813 mm; annual temperature (max. + min. /2): 21.8 ± 0.7, 21.4–22.3°C (N=2).

Habitat: No quantitative assessment; DBRU collection records primarily on sand (3), but also sandy loam (1) in shrubland (2) or open woodland (2).

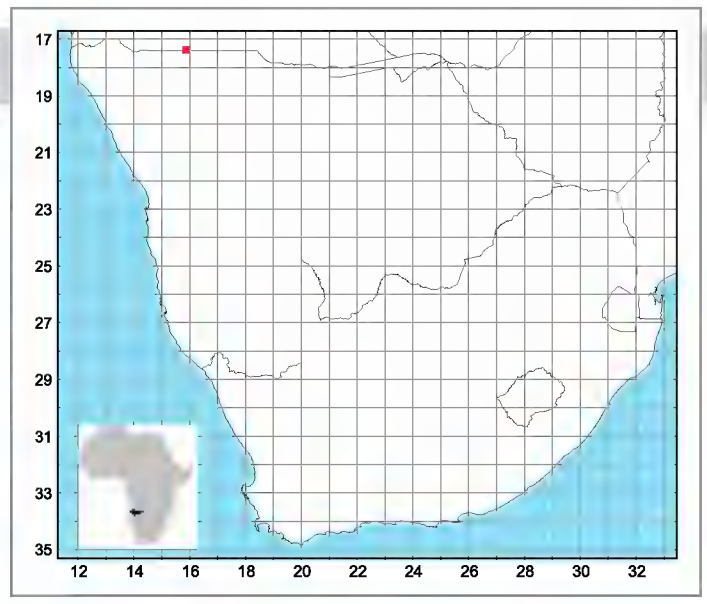
Food types: No quantitative assessment; DBRU collection records from the dung of cattle (3) and elephant (1).

Temporal activity: Presumed to show diurnal flight activity; recorded in the summer rainy season (Nov., Dec.).

Ecoregions Namibia: Angolan Mopane Woodlands (AT0702).

Assessment rationale: EOO = 197 250 km^2; AOO possibly more limited due to soil and woody vegetation habitat bias, but very poorly known ecologically; owing to limited data, assessed as Data Deficient (DD).

Conservation measures: To assess conservation status, a quantitative survey is required to determine the full EOO, AOO and ecological associations; protected in Bicuar National Park, Angola.



Genus *Proagoderus* van Lansberge, 1883

Type species and designation: *Onthophagus* (*Proagoderus*) *ritsemae* van Lansberge, 1883, by monotypy.

Synonyms:
= *Onthotrogus* Motschulsky, 1860; Type species: *Copris auratus* Fabricius, 1801, by monotypy (suppressed by ICZN 1993: Opinion 1708).
= *Melinocerus* Motschulsky, 1860; Type species: *Copris harpax* Fabricius, 1801, by monotypy (*nomen oblitum*).
= *Tauronthophagus* Shipp, 1895c: Type species: *Onthophagus rangifer* Klug, 1855, by original designation.

Last review: Reviewed as a subgenus of *Onthophagus* Latreille, 1802, by Palestrini (1992, all species); with revision of a species complex (Moretto 2004) and addition of new Afrotropical species by Josso and Prévost (2001), Moretto and Nicolas (2002, 2004), Moretto (2004, 2013b), Josso (2014).

Proagoderus van Lansberge, 1883, was described as a subgenus of *Onthophagus* Latreille, 1802. More recently, it has been cited as a genus (Cambefort 1991; Davis et al. 2008), but only formally raised to generic status by Moretto (2013b).

On the basis of long-term usage, the name has been conserved as *Proagoderus* despite the precedence of *Onthotrogus* Motschulsky, 1860, which has been suppressed and placed on the list of invalid names by the International Commission of Zoological Nomenclature (ICZN 1993: Opinion 1708). As *Proagoderus*, thus, becomes a protected name (*nomen protectum*), the forgotten name (*nomen oblitum*) of *Melinocerus* Motschulsky, 1860, may also be considered a synonym (Moretto 2013b) despite its precedence.

Proagoderus currently comprises 127 species primarily centred in the Afrotropical region (117) with a few centred in the Oriental region (10). The genus is divided into nine species groups (see Palestrini 1992) with such a range in morphology that each may deserve subgeneric or even generic status. A review of *Proagoderus* and its synonyms may thus be justified, as the four type species belong to different species groups.

In South Africa, Botswana and Namibia, *Proagoderus* is represented by 14 species belonging to seven groups. Six of these species belonging to Groups 2, 4, 5 or 7, are primarily associated with the dung of monogastric herbivores, e.g. elephant, zebra, accounting for the patchy distributions centred around game reserves.

In southern Africa:

1. Group *confossus*: Comprises three species; two with E savanna ranges in open woodland or dense woodland on clay soils; one other centred on SE coast and highland grassland of South Africa plus N Namibian uplands where it is a rarity.

2. Group *auratus*: One species with an E savanna range extending N into the E tropics.

3. Group *bicallosus*: One species with a savanna range extending N into the tropics.

4. Group *gibbiramus*: Two rare species with savanna or W savanna ranges.

5. Group *prostans*: One species with an E savanna range extending N into the E tropics.

6. Group *ramosicornis*: One species with E savanna range extending N into the E tropics.

7. Group *dives*: Comprises five species, four with ranges centred on the E coast sands: E coast forest (1), E coast grass plus E savanna (2), E coast plus E upland grasslands; the fifth centred on deep Kalahari sands.

Most *Proagoderus* species are assessed as Least Concern (LC) as they are widespread. However, with the exception of species showing Kalahari or highland ranges, most are more abundant in reserves than in farmland, particularly those that are frequently recorded on elephant or zebra dung. The members of the *gibbiramus* group are assessed as Data Deficient (DD) as they are recorded very infrequently, and then only in elephant dung in reserves.

Proagoderus aciculatus

(Fahraeus, 1857)

= *Onthophagus* (*Proagoderus*) *aciculatus* var. *ahenus* d'Orbigny, 1902

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Onthophagus aciculatus*: 'in terra Natalensi et prope fluvium Limpopo' [KwaZulu-Natal, South Africa, and near Limpopo River]; var. *ahenus*: 'Mozambique: Delagoa-Bay' [Maputo, Mozambique].

Taxonomy: Accepted *dives* group species; muted metallic colour variation from dull cupreous to dull green to dull blue.

Distribution: Vegetation offering shade on SE coastal sands: South Africa, Mozambique.

Locality data (mean ± SD, range): Altitude: 43 ± 58, 0–273 m; annual rainfall: 862 ± 120, 629–1 254 mm; annual temperature (max. + min. /2): 21.8 ± 1.2, 18.4–24.8°C (N=74).

Habitat: In uMkhuze Game Reserve: extreme bias to coarse-grained soils, deep sand (462.9), sand over clay (93.9), sandy clay loam (0.4), clay (1.3); on deep sand in Maputo Elephant Reserve: bias to cooler coastal dune forest (303.9), less abundant in warmer inland sand forest (large patch: 41.2; medium: 38.7; small: 24.3), rare in grassland (2.2); across a chronosequence of regenerating dune vegetation at Richards Bay: uncommon in 0–5 yr grassland (4.7), more abundant in 3–15 yr dense (18.3) or 12–33 yr open understorey woodland (38.0); largely supported by DBRU collection records: sand (23), sandy loam (1), sandy clay loam (1) in grassland (12), open woodland (7), forest (17).

Food types: No quantitative assessment; DBRU collection records on various dung types with possible bias to omnivore dung: human/human + cattle mix (13), horse (2), elephant (1), cattle (9).

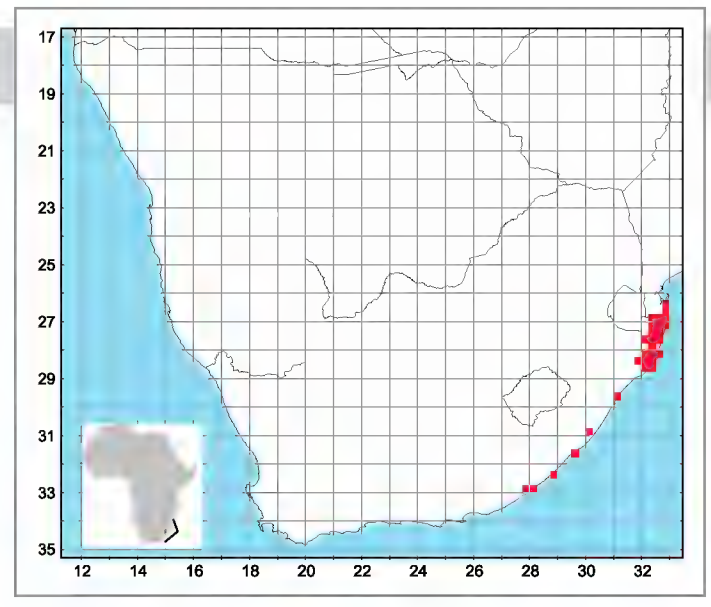
Temporal activity: Diurnal flight activity during much of the year (Aug. to May); observed to pitch on leaves in forest.

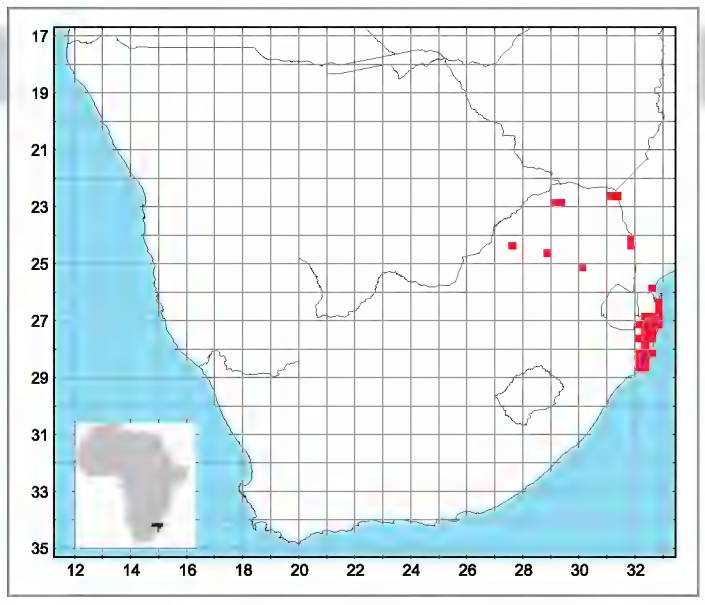
Ecoregions Mozambique: Maputaland Coastal Forest Mosaic (AT0119), Southern Zanzibar-Inhambane Coastal Forest Mosaic (AT0128) (not shown on map).

Bioregions South Africa: Centred on Indian Ocean Coastal Belt Biome (CB); SE margins of Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 33 450 km²; AOO smaller, restricted to shaded situations on moist E coastal sands; therefore, susceptible to clearance of forest or dense woodland for coastal development; in South Africa, vegetation units of the coastal belt are some 30–50% transformed by plantations, cultivation and urban sprawl (CB1, CB2); however, *P. aciculatus* is locally abundant and well protected in reserves; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on food type associations; protected in Hluhluwe–iMfolozi, uMkhuze game reserves (South Africa), Maputo Elephant Reserve (Mozambique).





Proagoderus aureiceps

(d'Orbigny, 1902)

= *Onthophagus sapphyrinus* Péringuey, 1901

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Onthophagus* (*Proagoderus*) *aureiceps*: 'Mozambique: district de Delagoa....Delagoa-Bay' [Maputo, Mozambique], lectotype: Maputo; *O. sapphyrinus*: 'Southern Rhodesia (Salisbury, Victoria Falls, Limpopo River), Ovampoland, (Okovango River, Humbe Omrramba), Transvaal (Rustenburg), Mozambique (Rikatla)' [Zimbabwe, South Africa, Mozambique].

Taxonomy: Accepted *dives* group species, but confusion in literature indicates that revision is required; *P. aureiceps* may be a junior synonym of *P. sapphirinus* (Fahraeus, 1857), whose name suggests a blue type specimen; details and cited localities for the synonym, *O. sapphyrinus* Fahraeus *sensu* Péringuey, include a green/blue coastal form (Rikatla) that would equate to *P. aureiceps*, but primarily comprises green individuals with yellow/red elytra that would belong to a different species (see species page for *P. sapphirinus* (Fahraeus, 1857)).

Distribution: Abundant on coastal sands in SE Mozambique and NE South Africa; also moister parts of Limpopo River Valley; uncommon in the N interior of South Africa where scattered records border the Soutpansberg and Waterberg and overlap with the closely related species (green with red elytra) that is currently listed under the name, *P. sapphirinus* (Fahraeus, 1857).

Locality data (mean ± SD, range): Altitude: 157 ± 303, 0–1 376 m; annual rainfall: 763 ± 148, 422–1 006 mm; annual temperature (max. + min. /2): 22.0 ± 1.0, 17.6–23.4°C (N=63).

Habitat: In uMkhuze Game Reserve: extreme bias to coarse-grained soils, deep sand (279.3), sand over clay (23.7), sandy clay loam (0.1), clay (0.2); on deep sand in Maputo Elephant Reserve: bias to grassland (54.8), much less abundant in warmer inland sand forest (large patch: 3.6; medium: 4.6; small: 3.5) and cooler coastal dune forest (1.0); across a chronosequence of regenerating dune vegetation at Richards Bay: primarily in 0–5 yr grassland (3.5), rare in 3–15 yr dense (0.1) or 12–33 yr open understorey woodland (0.2); largely supported by DBRU collection records: sand (16), sandy loam (4) in grassland (11), open woodland (9), forest (4).

Food types: No quantitative assessment; DBRU collection records on various dung types: human/human + cattle mix (4), elephant (1), horse (2), cattle (1), wildebeest (2).

Temporal activity: Diurnal flight activity; recorded primarily in the summer rainy season (Oct. to May).

Ecoregions Mozambique: Maputaland Coastal Forest Mosaic (AT0119), Southern Zanzibar-Inhambane Coastal Forest Mosaic (AT0128).

Bioregions South Africa: Centred primarily on the N Indian Ocean Coastal Belt Biome (CB); sand patches in Lowveld (SVl), Central Bushveld (SVcb) (Savanna Biome).

Assessment rationale: EOO = 192 750 km^2; AOO much smaller, range restricted to coastal sands where it is abundant and inland sand outliers where it is uncommon; in South Africa vegetation units of the coastal belt are some 30–50% transformed by plantations, cultivation and urban sprawl (CB1, CB2); centred on grassland habitats, so perhaps not that influenced by clearance of woody vegetation; abundant in reserves so assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on food type associations; protected in uMkhuze Game Reserve, iSimangaliso Wetland Park (World Heritage Site) (South Africa), Maputo Elephant Reserve (Mozambique).

Proagoderus bicallosus

(Klug, 1855)

= *Onthophagus metallicus* Fahraeus, 1857
= *Onthophagus* (*Proagoderus*) *bicallosus* var. *olivicolor* d'Orbigny, 1902

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Onthophagus bicallosus*: 'Sena' [central Mozambique]; *O. metallicus*: 'prope fluvium Limpopo' [near Limpopo River]; var. *olivicolor*: 'région du lac Tanganyika' [Lake Tanzania region].

Taxonomy: Accepted *bicallosus* group species; metallic colour variation from cupreous to green to olive; cupreous in southern Africa; minor sexual dimorphism (prothoracic disc).

Distribution: Widespread, but patchy occurrence across southern to E African lowland savannas owing to dung specialisation: NE South Africa, N Namibia, N Botswana, Angola, Zimbabwe, Mozambique, Tanzania, Kenya; also reported from Malawi, Zambia.

Locality data (mean ± SD, range): Altitude: 517 ± 401, 0–1 207 m; annual rainfall: 656 ± 122, 418–971 mm; annual temperature (max. + min. /2): 22.3 ± 0.9, 20.5–25.7°C (N=52).

Habitat: No quantitative assessment; DBRU collection records suggest a bias to coarser-grained soils: sand (7), sandy loam (6), in woody vegetation: open shrub-woodland (13), grassland (2).

Food types: In Botswana: strong bias to monogastric herbivore (elephant: 20) and omnivore dung (pig: 12), few on ruminant herbivore (cattle: 2; sheep: 2) and carrion (chicken livers: 0); partly supported by DBRU collection records: elephant (15), rhinoceros (3), donkey (1), cattle (6).

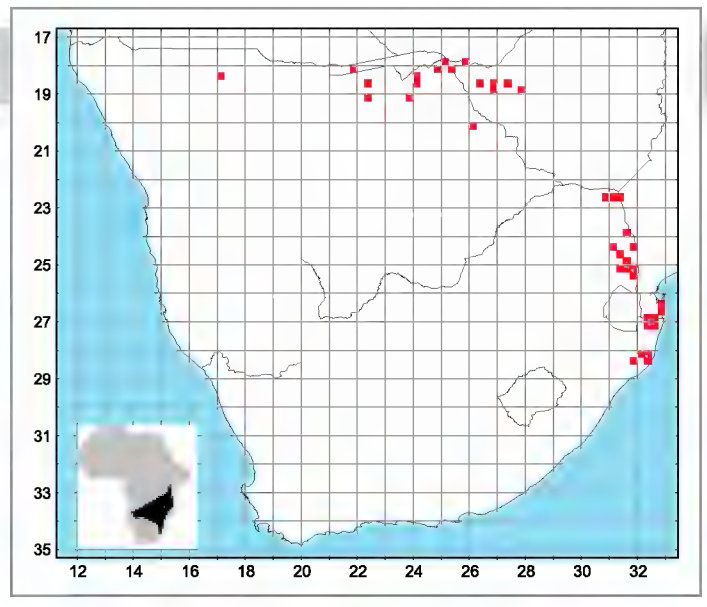
Temporal activity: Diurnal flight activity; recorded primarily in the summer rainy season (Oct. to Apr.), also Aug. at the warmer coastline.

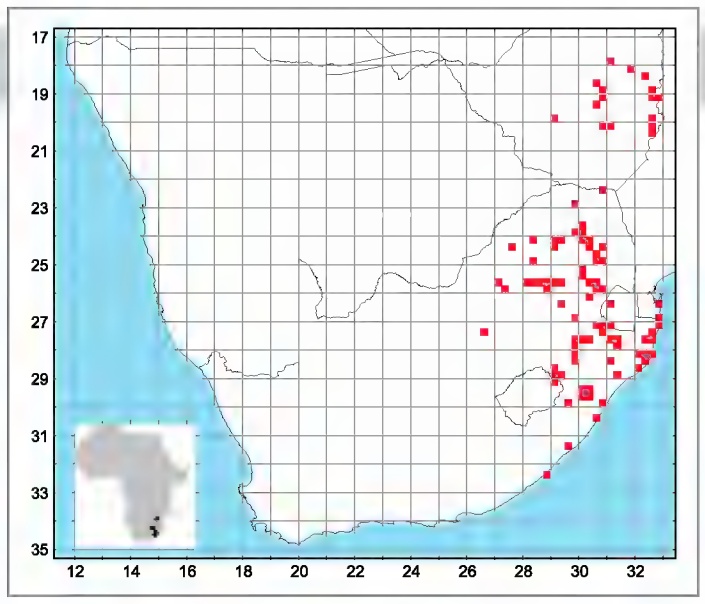
Ecoregions Namibia, Botswana, Zimbabwe, Mozambique:, Centred on Angolan Mopane Woodlands (AT0702), Zambezian and Mopane Woodlands (AT0725), Zambezian Baikiaea Woodlands (AT0726), Maputaland Coastal Forest Mosaic (AT0119).

Bioregions South Africa: Centred on Lowveld (SVl), Mopane (SVmp) (Savanna Biome).

Assessment rationale: EOO = 3 227 420 km^2; AOO would be much smaller since modern records (52 out of 68) are primarily from game reserves; recent records centred in two regions (see map); in South Africa: recent records only from reserves containing monogastric herbivores despite a secondary strong association with omnivore dung; at present assessed as Least Concern (LC) owing to widespread range and occurrence in many reserves.

Conservation measures: Assessment of conservation status would be improved by quantitative data on habitat associations to determine if AOO is influenced by soil and vegetation type specialisation; current AOO primarily restricted to reserves containing elephants and rhinoceros whose continuing protection would be of great importance for the conservation of this species; protected in various national parks and game reserves, including, Kruger, Hluhluwe–iMfolozi (South Africa), Chobe (Botswana), Manyara (Tanzania).





Proagoderus chalcostolus

(d'Orbigny, 1902)

= *Onthophagus* (*Proagoderus*) *brucei* var. *panchlorus* d'Orbigny, 1913

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Onthophagus* (*Proagoderus*) *brucei* var. *chalcostolus*: 'Natal.....Cap de Bonne-Espérance', lectotype: 'Natal'; var. *panchlorus*: Not stated, lectotype: 'Natal' [South Africa: KwaZulu-Natal and Cape of Good Hope; latter locality inexact].

Taxonomy: Accepted *dives* group species; metallic colour variation from cupreus to more frequent green; sexually dimorphic (head, prothoracic disc), characters vary in prominence with body size.

Distribution: Centred on moist uplands and moist coastal regions of SE Africa: NE South Africa, S Mozambique, Eswatini, E central Zimbabwe; Botswana record requires validation.

Locality data (mean ± SD, range): Altitude: 1 026 ± 587, 0–2 392 m; annual rainfall: 829 ± 150, 428–1 415 mm; annual temperature (max. + min. /2): 18.0 ± 2.6, 9.9–23.5°C (N=136).

Habitat: No quantitative assessment: DBRU collection records suggest a bias to finer-grained soils: clay (1), sandy clay loam (11), sandy loam (14), sand (5) in open vegetation: pasture/grassland (23), open woodland (5), forest (2); one record from a fallow crop field.

Food types: No quantitative assessment: DBRU collection records primarily from cattle dung (39), also dung of rhinoceros, horse, zebra, human, buck pellets (all 1, except horse: 2).

Temporal activity: Diurnal flight activity, primarily during the summer rainy season (Oct. to Apr.); also active in May at the warmer E coastline.

Ecoregions Zimbabwe, Mozambique: Maputaland Coastal Forest Mosaic (AT0119), Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Centred on Indian Ocean Coastal Belt Biome (CB); warmer NE Mesic Highveld Grassland (Gm), N Sub-Escarpment Grassland (Gs) (Grassland Biome); also moist upland islands (Waterberg, Soutpansberg) in Central Bushveld (SVcb) (Savanna Biome); margins of two adjacent bioregions.

Assessment rationale: EOO = 232 570 km^2; widespread in warm, moist upland grasslands dominated by farmland where it readily colonises the dung of domestic livestock, especially cattle; in South Africa: appreciable transformation due to tree plantations and cultivation in upland bioregions (0–69%, Gm; 10–50%, Gs), but also found along the coastline, much of which is protected; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, particularly possible effects of pasture improvement; protected along the SE coastline in iSimangaliso Wetland Park (World Heritage Site) (South Africa).

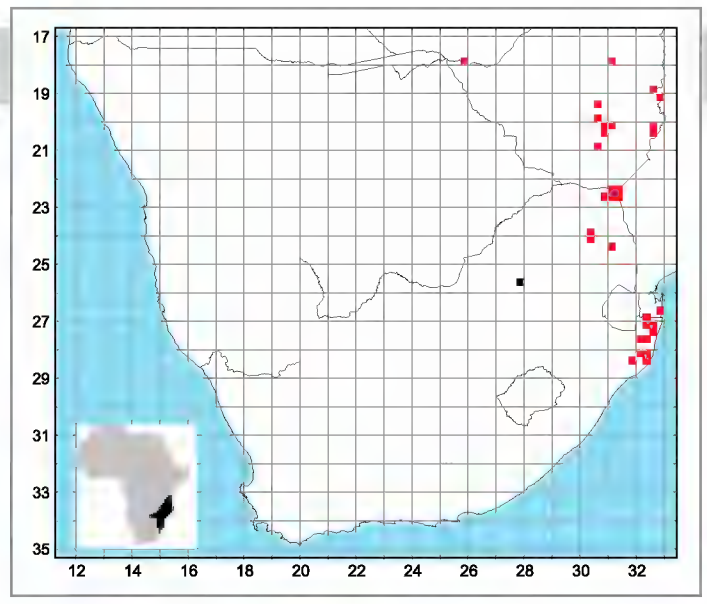
Proagoderus dives

(Harold, 1877b)

= *Onthophagus deyrollei* Raffray, 1877
= *Onthophagus optivus* Péringuey, 1901
= *Onthophagus* (*Proagoderus*) *dives* var. *funereus* d'Orbigny, 1902
= *Onthophagus* (*Proagoderus*) *dives* var. *semicuprinus* d'Orbigny, 1913

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: As *Onthophagus dives*: 'Nyassa', lectotype: Nyassa [Lake Malawi region]; *O. deyrollei*: 'Zanguebar, Bagamoyo' [Bagamoyo, NE Tanzania]; *O. optivus*: 'Southern Rhodesia (Mtoko)' [Zimbabwe]; var. *funereus*: 'M'honda dans l'Ouzigoua' [Mhonda, Tanzania]; var. *semicuprinus*: Not stated.

Taxonomy: Accepted *dives* group species, metallic colour variation from cupreous to green to blue, even black; in southern Africa: cupreous inland, green to blue on the coast.

Distribution: Widespread, but somewhat patchy distribution across moist savanna from southern to E Africa, probably due to soil and vegetation specialisation: South Africa, Mozambique, Zimbabwe, Zambia, Tanzania; also reported from Malawi; Kenyan record requires validation; black square represents a questionable record.

Locality data (mean ± SD, range): Altitude: 411 ± 436, 0–1 410 m; annual rainfall: 805 ± 211, 383–1 270 mm; annual temperature (max. + min. /2): 22.1 ± 2.1, 17.1–25.9°C (N=57).

Habitat: In uMkhuze Game Reserve: extreme bias to coarse-grained soils, deep sand (125.0), sand over clay (22.5), sandy clay loam (0.1), clay (0.1); no quantitative assessment of vegetation association; DBRU collection records support a bias to coarse-grained soil association: sand (16), sandy loam (3), sandy clay loam (4), in shaded vegetation: forest (14), open woodland (16), grassland/pasture (6).

Food types: No quantitative assessment; DBRU collection records on various dung types with possible bias to omnivore dung: human/human + cattle mix (14), baboon (3), elephant (2), rhinoceros (2), horse (3), cattle (9), wildebeest (1).

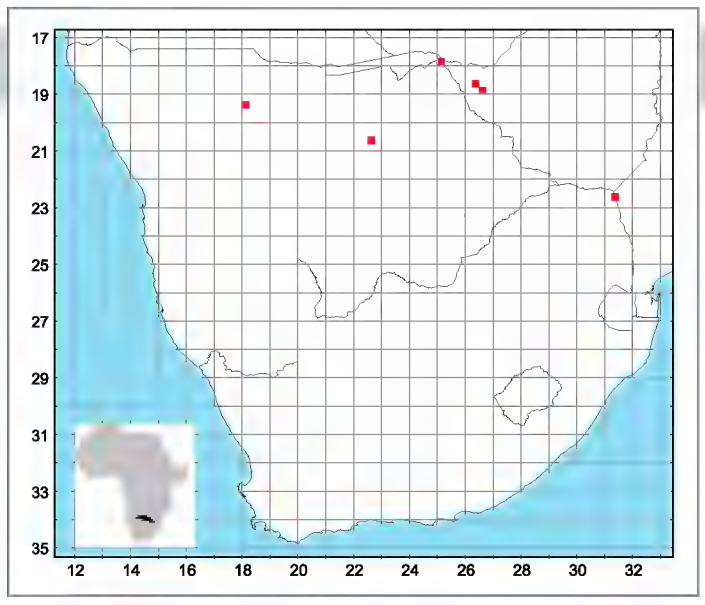
Temporal activity: Diurnal flight activity during the summer rainy season (Oct. to Apr.)

Ecoregions Zimbabwe, Mozambique: Zambezian and Mopane Woodlands (AT0725), Southern Miombo Woodlands (AT0719), Maputaland Coastal Forest Mosaic (AT0119).

Bioregions South Africa: Centred primarily on N Indian Ocean Coastal Belt Biome (CB); sand patches with shady vegetation in Lowveld (SVl), Mopane (SVmp) (Savanna Biome).

Assessment rationale: EOO = 1 444 830 km²; AOO presumably much smaller due to sand and shade specialisation; widespread, but cupreous variety uncommon near Tzaneen (South Africa) where there has been much vegetation transformation; also in South Africa, green variety abundant in coastal shade on deep sand; therefore, assessed as Least Concern (LC).

Conservation measures: Presumably, protection of dense woody vegetation on deep sand patches would be essential for the conservation of this species; however, assessment of conservation status would be improved by quantitative data on vegetation and food type association; cupreous variety protected in the N Kruger National Park, green variety protected in uMkhuze Game Reserve and iSimangaliso Wetland Park (World Heritage Site) (South Africa).



Proagoderus furcifer

(Boheman, 1860)

No synonyms

Global: DD

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Onthophagus furcifer*: 'juxta lacum N'Gami' [near Lake Ngami, Botswana].

Taxonomy: Accepted *gibbiramus* group species; *Onthophagus plato* Bates, 1888, made a synonym by Péringuey (1901), but considered incorrect; strong sexual dimorphism (head, prothoracic disc), prominence of characters varies with body size.

Distribution: Dry southern African savanna woodlands: South Africa, Zimbabwe, Botswana, Namibia.

Locality data (mean ± SD, range): Altitude: 951 ± 280, 429–1 364 m; annual rainfall: 555 ± 85, 414–672 mm; annual temperature (max. + min. /2): 22.2 ± 0.7, 21.2–23.1°C (N=7).

Habitat: No quantitative assessment; limited DBRU and UP collection records inconclusive; sand (2), sandy loam (3), clay (1) in shrubland (1), open woodland (3), fallow crop field (1).

Food types: No quantitative assessment; limited DBRU collection records primarily on monogastric herbivore dung: elephant (3), rhinoceros (1), cattle (1).

Temporal activity: Diurnal flight activity during the summer rainy season (Nov to Mar.); observed flying early in the day.

Ecoregions Namibia, Botswana, Zimbabwe: Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian and Mopane Woodlands (AT0725), Zambezian Baikiaea Woodlands (AT0726).

Bioregions South Africa: Deep sand patch in Mopane (SVmp) (Savanna Biome).

Assessment rationale: EOO = 267 405 km^2; AOO probably much smaller; rarely observed; of six recent records, five in national parks, one caught flying and four on elephant or rhinoceros dung; probably a monogastric dung specialist, possibly on coarse-grained sandy soils in woodland; owing to its rarity and likely specialisation, probably deserves a threat category, but currently assessed as Data Deficient (DD) owing to limited records.

Conservation measures: A quantitative survey is required to better determine the EOO, ecological associations and AOO of this species before an accurate assessment may be made of its conservation status; however, currently protected in several national parks: N Kruger (South Africa), Hwange (Zimbabwe), Chobe (Botswana).

Proagoderus lanista

(Castelnau, 1840)

= *Onthophagus tubericollis* Castelnau, 1840
= *Onthophagus aulicus* Fahraeus, 1857
= *Onthophagus laniger* Chevrolat *in litt*. Harold, 1867c

Global: LC
Endemic: RSA, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Ontophagus lanista*: 'Cap de Bonne-Espérance' [Cape of Good Hope, South Africa]; *O. tubericollis*: 'Cap de Bonne-Espérance'; *O. aulicus*: 'in terra Natalensi' [KwaZulu-Natal, South Africa]; *O. laniger*: Not stated.

Taxonomy: Accepted *confossus* group species; strong sexual dimorphism (head, prothoracic disc); prominence of characters varies with body size.

Distribution: Highveld and SE coastline of South Africa with limited scattered records on the plateau of N Namibia; records reported for Botswana and Zambia considered of doubtful validity.

Locality data (mean ± SD, range): Altitude: 1 193 ± 491, 0–2 199 m; annual rainfall: 672 ± 173, 305–982 mm; annual temperature (max. + min. /2): 16.7 ± 2.3, 11.2–22.3°C (N=73).

Habitat: No adequate quantitative assessment; at Foggy Valley: primarily in natural *Themeda* grassland (21), few in disturbed regenerating vegetation of crop fields (4) or improved Kikuyu pasture (0); DBRU collection records suggest bias to finer-grained soils: sand (3), sandy loam (11), sandy clay loam (14), clay (3) in open vegetation: pasture/grassland (19), scrub/shrubland (3), open woodland (1); few in fallow crop fields (2).

Food types: No quantitative assessment; DBRU collection records primarily on cattle dung (32); also horse (1) and zebra dung (2).

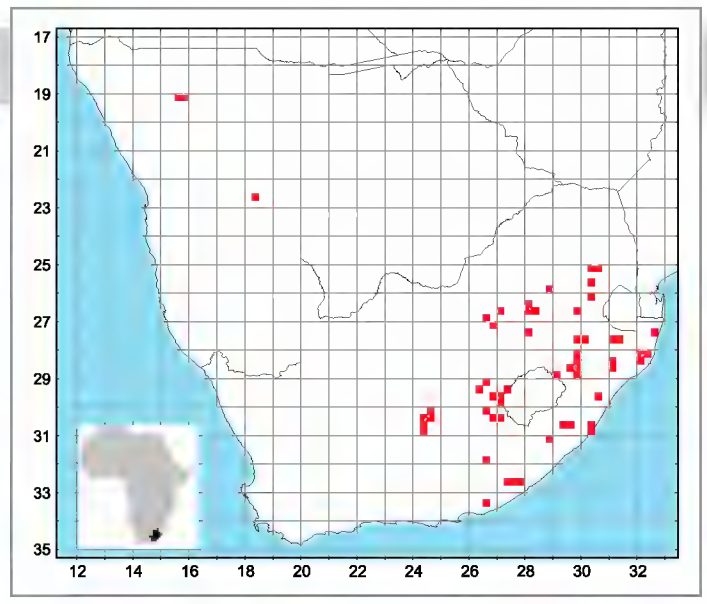
Temporal activity: Diurnal flight activity during the summer rainy season (Oct. to Apr.); also Aug. and May on warmer NE coastline.

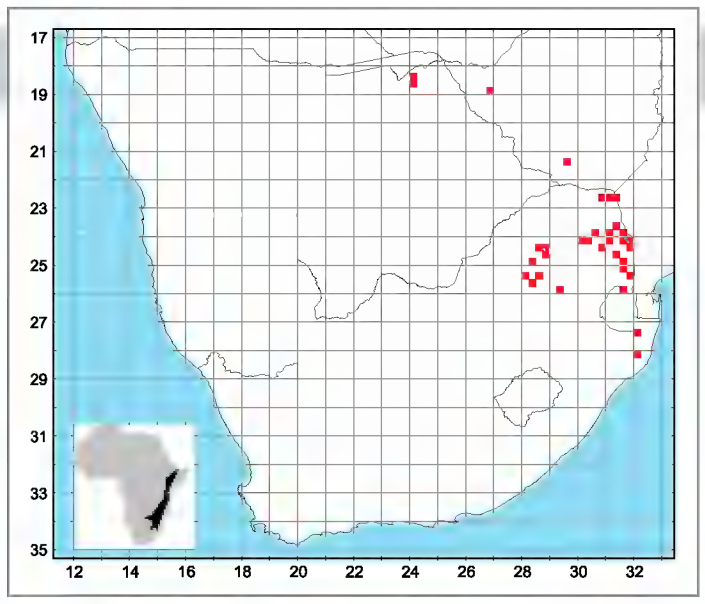
Ecoregions Namibia: NW Kalahari Xeric Savanna (AT1309), Angolan Mopane Woodlands (AT0702).

Bioregions South Africa: Centred on Indian Ocean Coastal Belt Biome (CB); Sub-Escarpment Savanna (SVs) (Savanna Biome), E Dry Highveld Grassland (Gh), Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs) (Grassland Biome); marginal occurrence in two adjacent bioregions.

Assessment rationale: EOO = 300 285 km^2; uncommon on N plateau of Namibia but commonly found in cattle dung on farms across the Highveld grasslands of South Africa; results from Foggy Valley suggest that habitat transformation, including pasture improvement, are detrimental; transformation through cultivation and development of tree plantations varies from 4 to 60% (Gh), 6–69% (Gm) and 2–50% (Gs); nevertheless, widespread in SE South Africa; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by further quantitative data on ecological associations; limited data suggest protection from pasture improvement within nature reserves would be advantageous to the conservation of this species; protected in Ithala Game Reserve, Suikerbosrand Nature Reserve (South Africa); Etosha National Park (Namibia).





Proagoderus loricatus

(Klug, 1855)

= *Onthophagus collaris* Fahraeus, 1857
= *Onthophagus harpax* Fabricius, 1801, *sensu* Gestro, 1895

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Onthophagus loricatus*: Not stated; *O. collaris*: 'juxta fluvium Gariep' [near Orange River, South Africa]; *O. harpax sensu* Gestro: 'Boran Galla, Auata' [Mount Auata, Boran Galla, Ethiopia].

Taxonomy: Accepted *auratus* group species, but validation of NE African synonym would be useful; limited sexual dimorphism (head).

Distribution: Widespread from SE to NE Africa; occurrence now patchy, mainly centred on game reserves in dry savanna: South Africa, N Botswana, Zimbabwe. Mozambique, Kenya; also reported from Tanzania, Uganda; records from Somalia, Ethiopia overlap with range of close relative, *P. harpax* (Fabricius, 1801).

Locality data (mean ± SD, range): Altitude: 595 ± 367, 92–1 524 m; annual rainfall: 604 ± 94, 428–900 mm; annual temperature (max. + min. /2): 21.4 ± 1.8, 15.6–25.9°C (N=51).

Habitat: No conclusive data: in open woodland at Leeuwfontein Nature Reserve: sand (10), sandy loam (2), stony sandy loam (2); DBRU collection records: sand (2), sandy loam (5), sandy clay loam (1) in shrubland (1), open woodland (3), shaded thicket (1).

Food types: At Phalaborwa: strong bias to omnivore dung (pig: 32) compared to herbivore dung (elephant: 2; cattle: 1); similar in Botswana: pig (21), elephant (3), cattle (2), sheep (3); however, DBRU collection records support strong influence of monogastric herbivore dung on distribution pattern: elephant (8), donkey (1); few records on ruminant herbivore dung: cattle (2).

Temporal activity: Diurnal flight activity during the summer rainy season (Oct. to Mar.); at Phalaborwa: frequency much greater in hot, dry conditions (28) than in warm cloudy conditions following light rainfall (2) or in warm sunny conditions soon after heavy rainfall (5).

Ecoregions Botswana, Zimbabwe: Zambezian and Mopane Woodlands (AT0725), Zambezian Baikiaea Woodlands (AT0726).

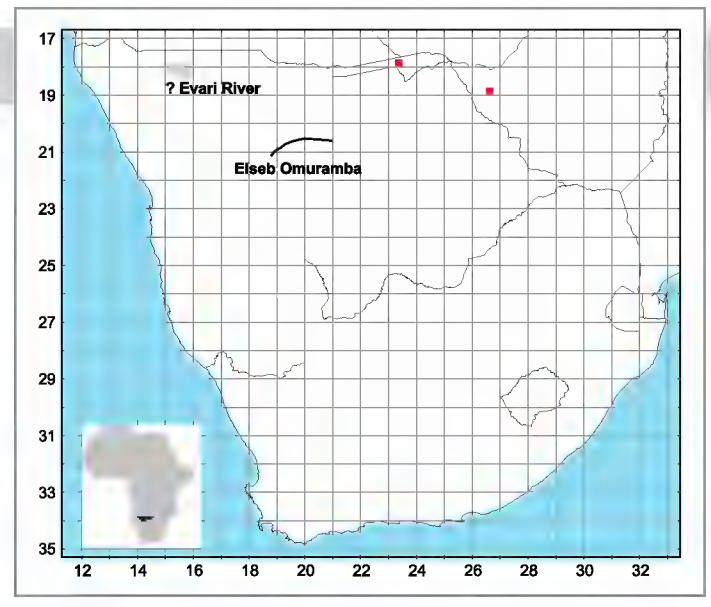
Bioregions South Africa: Centred on Central Bushveld (SVcb), Lowveld (SVl), Mopane (SVmp) (Savanna Biome).

Assessment rationale: EOO = 1 895 725 km²; despite measured food type bias, AOO probably much reduced due to range contraction by monogastric herbivores; 65% of DBRU collection records (11/17) were from game reserves; in South Africa, most modern records are from two centres, environs of Kruger National Park and bushveld nature/game reserves containing zebra; assessed as Least Concern (LC) due to wide distribution in many reserves.

Conservation measures: Assessment of conservation status would be improved by further quantitative data on ecological associations, owing to the inconclusive and conflicting information currently available; protected in various national parks, including Kruger (South Africa), Hwange (Zimbabwe), Chobe (Botswana).

Proagoderus plato

(Bates, 1888)



No synonyms

Global: DD (see IUCN Red List – DD)

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Onthophagus plato*: 'Damaraland' [inexact, N Namibia – defined at the time of collection as lying between 19–23°S and 14–20°E (Bates 1888)].

Taxonomy: Accepted *gibbiramus* group species described from a single male specimen; male specimen cited here as *P. plato* requires validation by comparison with the type; female specimens need to be confirmed as those of *P. plato*; they show arcuate clypeal margins that differ from those of *P. furciger* by lacking a mid-clypeal projection; also see notes on former synonymy of *P. plato* on species page for *P. furcifer* (Boheman, 1860); strong sexual dimorphism (head, prothoracic disc); prominence of characters varies with body size.

Distribution: Dry savanna from N Namibia to W Zimbabwe; black line represents inexact origin of a male specimen (Eiseb Omuramba – Omuramba = a dry watercourse), all other data points and shaded areas represent female specimens.

Locality data (mean ± SD, range): Altitude: 1 023 ± 111, 945–1 102 m; annual rainfall: 613 ± 21, 598–628 mm; annual temperature (max. + min. /2): 21.6 ± 0.6, 21.2–22.1°C (N=2); Evari and Eiseb similar except drier (annual rainfall: 385 ± 14, 371–398 mm).

Habitat: No quantitative assessment; one DBRU record for females from sandy loam in open mopane woodland.

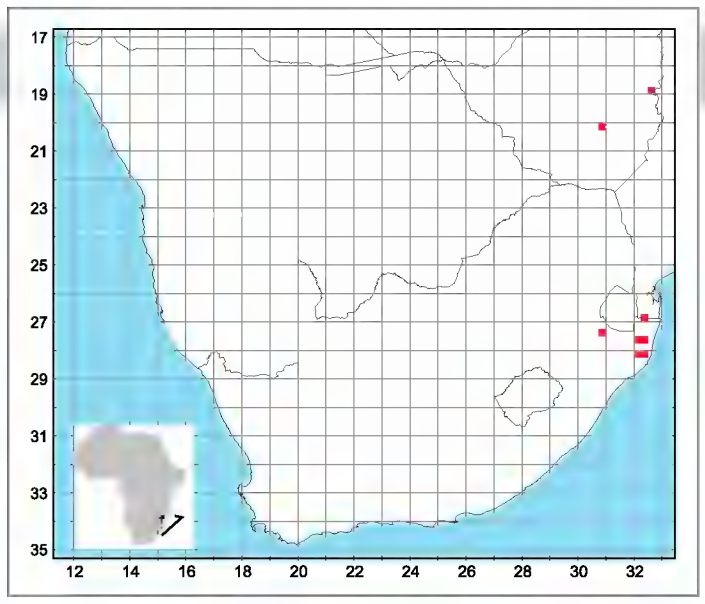
Food types: No quantitative assessment; one DBRU record for females from elephant dung.

Temporal activity: Presumed to show diurnal flight activity during the summer rainy season like other *Proagoderus* species in southern Africa (Nov., Apr.).

Ecoregions Namibia, Zimbabwe: Zambezian Baikiaea Woodlands (AT0726: red squares), Angolan Mopane Woodlands (AT0702), Kalahari Acacia-Baikiaea Woodlands (AT0709).

Assessment rationale: EOO = 235 670 km^2 (tentative); species of the *gibbiramus* group are usually recorded as rarities from elephant dung; the few individuals treated here as *P. plato* may equally represent the same or a different species; two specimens were collected from within the area of the inexact type locality, the male and one old record for a female (Evari River =?upper reaches of Etaka River, NW of Etosha Pan); assessed as Data Deficient (DD).

Conservation measures: Specimens cited here need to be validated as *P. plato* by comparison with the type and by acquisition of further reference material from Damaraland eastwards to W Zimbabwe; such a survey is also required to determine the EOO, AOO and ecological associations before an accurate assessment may be made of conservation status; possibly protected in Hwange National Park along with *P. furcifer*.



Proagoderus quadrituber

(d'Orbigny, 1908)

No synonyms

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Onthophagus* (*Proagoderus*) *quadrituber*: 'Zambèze: Chindé...Mozambique: vallée de Pungoué...Sikumba', lectotype: Guengère [all central Mozambique].

Taxonomy: Accepted *confossus* group species; strong sexual dimorphism (head, prothoracic disc); prominence of characters varies with body size.

Distribution: Widespread, but very patchy SE African occurrence due to soil and woody vegetation specialisation: South Africa, Zimbabwe, Mozambique, Malawi.

Locality data (mean ± SD, range): Altitude: 315 ± 447, 2–1 377 m; annual rainfall: 858 ± 178, 634–1 177 mm; annual temperature (max. + min. /2): 21.6 ± 2.2, 17.3–25.2°C (N=11).

Habitat: In uMkhuze Game Reserve: strongly biased to clay (2.3) rather than sandy clay loam (0.0), or sand (0.3); some support from DBRU collection records on clay (3), sandy clay loam (2), sand (1) in forest (1), woodland (2), shrubland (1), grassland (2).

Food types: No quantitative assessment; DBRU collection records on various dung types: human/cattle mix (2), rhinoceros (3), cattle (2).

Temporal activity: Diurnal flight activity, primarily during the summer rainy season (Oct. to Apr.); also Aug. in warm coastal KwaZulu-Natal.

Ecoregions Zimbabwe: Southern Miombo Woodlands (AT0719); also riverine locality in Zambezian and Mopane Woodlands (AT0725).

Bioregions South Africa: Moist S Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 134 250 km^2; AOO probably a small fraction of the EOO reflecting restricted extent of clay; if this species is associated with dense woody vegetation, clearance would be detrimental; in South Africa, vegetation units within the known species range are 22–26% transformed; however, currently assessed as Least Concern (LC) owing to protection offered by reserves.

Conservation measures: Assessment of conservation status would be improved by quantitative data to better support association with dense woody vegetation, and a survey of densely vegetated clay patches in SE Africa to better determine the EOO and AOO; existing records mostly from protected game reserves, such as Lake Mutirikwe (Zimbabwe), uMkhuze, Hluhluwe–iMfolozi (South Africa).

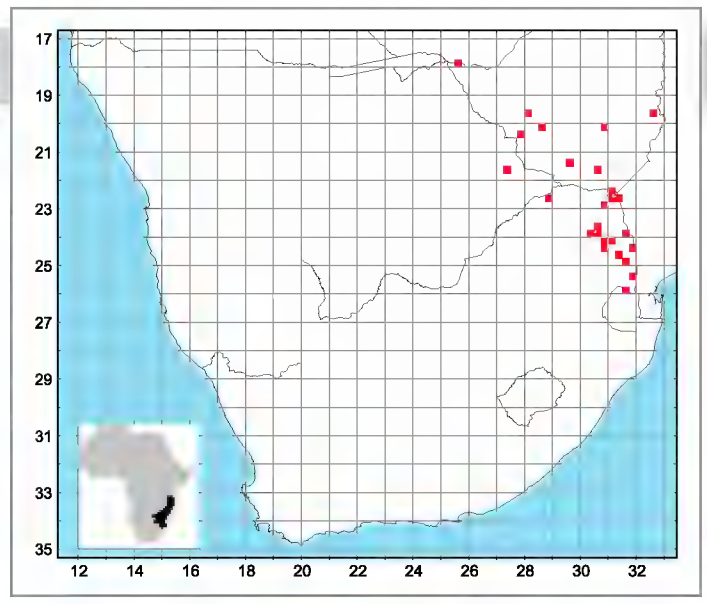
Proagoderus rangifer

(Klug, 1855)

= *Onthophagus bradshawi* Péringuey, 1885

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: As *Onthophagus rangifer*: 'in den ebenen von Sena und in Caya häufig' [common on the plains of Sena and Caia, central Mozambique]; *O. bradshawi*: 'Zambezi River' [southern Africa].

Taxonomy: Accepted *ramosicornis* group species; N limits of distribution reported to be in Tanzania, presumably to the S of the range occupied by the very closely related *P. ramosicornis* d'Orbigny, 1902 in Kenya and Tanzania; reconsideration of the differences between these two species would be useful; strong sexual dimorphism (head, prothoracic disc); prominence of characters varies with body size; iridescent colour variation from cupreous to green.

Distribution: Widespread in SE Africa; occurrence now patchy, centred in dry savanna, mainly in game reserves or areas with sizeable equine populations: South Africa, NW Botswana, Zimbabwe, Mozambique; also reported from Namibia, Malawi, Tanzania.

Locality data (mean ± SD, range): Altitude: 586 ± 341, 61–1 478 m; annual rainfall: 598 ± 139, 317–1 100 mm; annual temperature (max. + min. /2): 21.9 ± 1.7, 16.7–25.7°C (N=35).

Habitat: No quantitative assessment; DBRU collection records from sand (1), sandy loam (6), sandy clay loam (1) in pasture (1), shrubland (2), open woodland (3).

Food types: At Phalaborwa: much more abundant on omnivore dung (pig: 41) than herbivore dung (elephant: 2; cattle: 2); DBRU collection records from dung of elephant (2), rhinoceros (1), donkey (2), cattle (4), waterbuck (1).

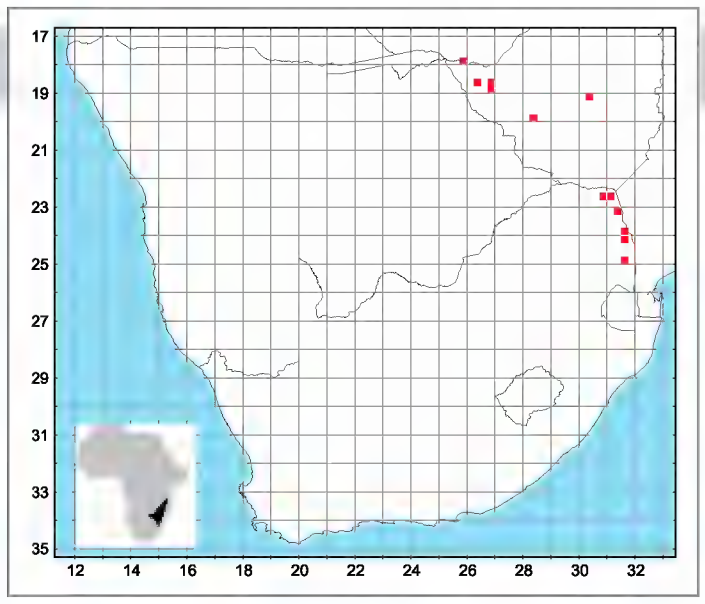
Temporal activity: Diurnal flight activity during the summer rainy season (Oct. to Mar.); at Phalaborwa: frequency much greater in warm sunny conditions soon after heavy rainfall (33) than in hot, dry conditions (11) or warm cloudy conditions following light rainfall (2).

Ecoregions Botswana, Zimbabwe: Southern African Bushveld (AT0717), Zambezian and Mopane Woodlands (AT0725), margins of Southern Miombo Woodlands (AT0719).

Bioregions South Africa: N Lowveld (SVl), Mopane (SVmp) (Savanna Biome).

Assessment rationale: EOO = 1 303 445 km^2; AOO probably much smaller owing to contraction in the range of indigenous monogastric herbivores despite quantitative data that suggest a bias to omnivore dung or collection records that suggest equal numbers from monogastric and ruminant herbivore dung; in South Africa, distribution centred around and within the Kruger National Park; however, currently assessed as Least Concern (LC) owing to wide distribution and adequate protection.

Conservation measures: Conservation status difficult to assess owing to inconclusive and conflicting data; further quantitative data on ecological associations are required to support possible effects of range contraction of monogastric herbivores and clearance of woody vegetation with which it may be associated; protected in Kruger National Park (South Africa).



Proagoderus rectefurcatus

(Fairmaire, 1891)

= *Onthophagus porrectus* Fahraeus, 1857 [pre-occupied name]
= *Onthophagus* (*Proagoderus*) *rectefurcatus* var. *metallarius* d'Orbigny, 1913

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Onthophagus rectefurcatus*: 'Mrogoro' [Morogoro, Tanzania]; *O. porrectus* Fahraeus: 'prope fluvium Limpopo' [near Limpopo River]; var. *metallarius*: Not stated.

Taxonomy: Accepted *prostans* group species; strong sexual dimorphism (head, prothoracic disc); prominence of characters varies with body size; iridescent colour variation from cupreous to green; usually green.

Distribution: Widespread from SE to E Africa; occurrence now patchy, mainly centred on game reserves in dry savanna: South Africa, Zimbabwe, Tanzania; also reported from Botswana, Malawi, Zambia, Mozambique; record from Kenya requires validation.

Locality data (mean ± SD, range): Altitude: 630 ± 365, 266–1 247 m; annual rainfall: 580 ± 80, 435–697 mm; annual temperature (max. + min. /2): 22.5 ± 1.5, 19.3–25.9°C (N=20).

Habitat: No quantitative assessment; DBRU collections records from sand (1), sandy loam (5) in shrubland (2), open woodland (2).

Food types: No quantitative assessment; DBRU collections records from dung of elephant (13), rhinoceros (1), cattle (2).

Temporal activity: Diurnal flight activity in the summer rainy season (Nov. to Mar.).

Ecoregions Zimbabwe: Centred on Zambezian and Mopane Woodlands (AT0725); marginal in two adjoining ecoregions.

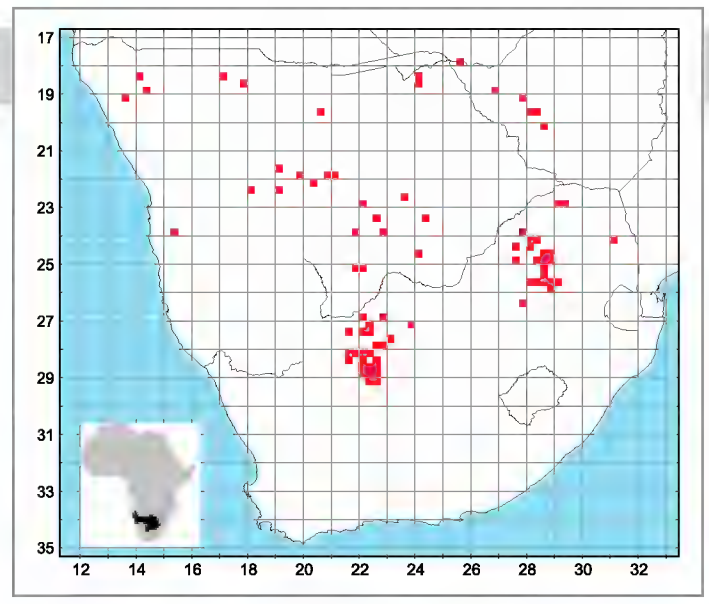
Bioregions South Africa: N Lowveld (SVl), Mopane (SVmp) (Savanna Biome).

Assessment rationale: EOO = 847 660 km^2; AOO much more range restricted, probably due to association with dung of large monogastric herbivores; 78% of DBRU collection records (14 out of 18) from game reserves; in South Africa, known only from Kruger National Park; widespread, but regularly found in dry savanna reserves containing elephants; therefore, currently assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; however, continued protection of large monogastric herbivores (elephant, rhinoceros) and woodland habitat on finer-grained soils probably essential for the conservation of this species; protected in several national parks including Kruger (South Africa), Hwange (Zimbabwe).

Proagoderus sapphirinus

(Fahraeus, 1857)



No synonyms

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Onthophagus sapphirinus*: 'juxta fluvium Limpopo' [near Limpopo River, southern Africa].

Taxonomy: Accepted *dives* group species, but confusion in literature indicates that revision is required; name possibly invalid as the Limpopo type specimen is blue and possibly a senior name for the green/blue Limpopo/E coastal *P. aureiceps* d'Orbigny, 1902; this Kalahari species is green with yellow/cupreous elytra, has more extensive and denser punctation than *P. aureiceps*, and may have no valid name (see species page for *P. aureiceps* d'Orbigny).

Distribution: Centred on continuous S Kalahari deep sands and outliers; NW South Africa, Botswana, Namibia; S Angola, S Zambia, central Mozambique; in the E: occurs inland in Kalahari outliers and on E coast at mouth of the Zambezi Valley; in the W: extends to edge of Namib Desert; in S Angola and S Zambia: overlaps with blue *P. speculicollis* Quedenfeldt, 1884; in NE South Africa and on SE Mozambique coast: overlaps with green/blue *P. aureiceps* d'Orbigny.

Locality data (mean ± SD, range): Altitude: 1 111 ± 187, 0–1 624 m; annual rainfall: 411 ± 176, 56–1 254 mm; annual temperature (max. + min. /2): 19.6 ± 1.2, 16.2–24.6°C (N=131).

Habitat: In Gauteng bushveld: extreme sand specialist (381), sandy clay loam (0) in grassland (151), open woodland (172), shaded thickets (58); largely supported by DBRU collection records: sand (19), sandy loam (6) in grassland/pasture (12), scrub/shrubland (7), open woodland (7).

Food types: In Botswana: bias to omnivore dung (pig: 48) rather than carrion (chicken livers: 14) and herbivore dung (elephant: 12; cattle: 9; sheep: 7); similar in Gauteng bushveld: carrion (54), dung of pig (87), horse (35), cattle (36), also rotted grass clippings (5) and overripe banana (8); DBRU collection records reflect common dung types: elephant (3), zebra (1), horse (1), donkey (1), cattle (13), waterbuck (1).

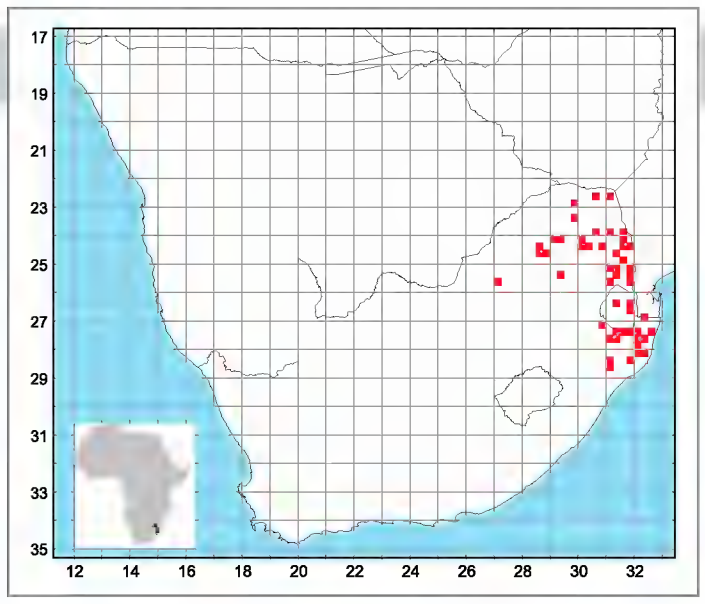
Temporal activity: Diurnal flight activity during the summer rainy season (Oct. to Apr.).

Ecoregions Namibia, Botswana, Zimbabwe: Centred on deep sands in Kalahari Xeric Savanna (AT1309), Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian Baikiaea Woodlands (AT0726); marginal in Namibian Savanna Woodlands (AT1316), Angolan Mopane Woodlands (AT0702), Zambezian and Mopane Woodlands (AT0725).

Bioregions South Africa: Centred on E Kalahari Duneveld (SVkd), W Eastern Kalahari Bushveld (SVk), sand patches in Central Bushveld (SVcb) (Savanna Biome).

Assessment rationale: EOO = 1 117 105 km^2; as a sand specialist, AOO would be limited to areas and patches of deep sands, which are, nevertheless, extensive across its EOO; much of range coincides with little-transformed regions used primarily for grazing of domestic livestock; data indicate a widespread vegetation and food generalist; therefore, assessed as Least Concern (LC).

Conservation measures: It is necessary to ensure that the species name is valid as it is possible that past errors may have resulted in this taxon being represented by a type specimen belonging to a different species; protected in the private Tswalu Kalahari Reserve (South Africa), Central Kalahari Game Reserve (Botswana), Hwange National Park (Zimbabwe).



Proagoderus tersidorsis

(d'Orbigny, 1902)

No synonyms

Global: LC
Endemic: RSA, Eswatini

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Onthophagus* (*Proagoderus*) *tersidorsis*: 'Natal' [KwaZulu-Natal, South Africa].

Taxonomy: Accepted *confossus* group species; strong sexual dimorphism (head, prothoracic disc); prominence of characters varies with body size.

Distribution: Centred on moist lowland savanna in NE South Africa and Eswatini.

Locality data (mean ± SD, range): Altitude: 532 ± 421, 0–1 694 m; annual rainfall: 697 ± 108, 448–932 mm; annual temperature (max. + min. /2): 20.7 ± 1.9, 15.1–23.1°C (N=74).

Habitat: In uMkhuze Game Reserve: biased to sandy clay loam (32.3) as opposed to deep sand (3.4), sand over clay (8.0) or clay (1.0); largely supported by DBRU collection records: sand (3), sandy loam (7), sandy clay loam (5), clay (3) in grassland/pasture (3), open woodland (8), shaded thickets (1).

Food types: No quantitative assessment; DBRU collection records on various dung types: baboon (1), elephant (4), rhinoceros (2), zebra (2), horse (1), donkey (1), cattle (12), wildebeest (2), impala (1).

Temporal activity: Diurnal flight activity, primarily during the summer rainy season (Oct. to Apr.).

Bioregions South Africa: Centred on Lowveld (SVl), scattered records from Central Bushveld (SVcb) (Savanna Biome); marginal in three other bioregions.

Assessment rationale: EOO = 85 690 km^2; AOO probably more restricted due to soil type specialisation and possible woody vegetation association; the possibility of reduced population density in response to clearance of woodland needs to be tested; however, as 66% (25 out of 38) of DBRU collection records are from game reserves, this species is currently assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by further quantitative data on ecological associations; protected in uMkhuze and Hluhluwe–iMfolozi game reserves plus Kruger National Park.

TRIBE SCARABAEINI

Latreille, 1802

As Scarabaeïdes; Type genus: *Scarabaeus* Linnaeus, 1758.

Synonyms:

Pachysomides Ferreira, 1953a; Type genus: *Pachysoma* Macleay, 1821.

Actinophorini Ádám, 2003; Type genus: *Actinophorus* Creutzer, 1799 [=*Scarabaeus* Linnaeus, 1758, senior name].

The tribe Scarabaeini is probably monophyletic. It shows a distribution centred on the winter rainfall, arid summer rainfall and savanna regions of the Afrotropical, S to E Palaearctic and W Oriental regions. Most species show either diurnal or nocturnal ball-rolling activity, although some show other specialisations. Recent generic and subgeneric subdivision of the tribe has been subject to different treatments by different authors.

Forgie et al. (2005) reduced 11 valid genera to only two, *Pachylomera* Griffith & Pidgeon, 1831, and *Scarabaeus* Linnaeus, 1758. Of the nine genera synonymised with *Scarabaeus*, some were made full synonyms: *Neateuchus* Gillet, 1911; *Drepanopodus* Janssens, 1940b; plus most flightless genera: *Mnematium* Macleay, 1821; *Mnematidium* Ritsema, 1888; *Neomnematium* Janssens, 1938a; *Madateuchus* Paulian, 1953). Others were reduced to subgeneric status: *Pachysoma* Macleay, 1821; *Sceliages* Westwood, 1837b; *Kheper* Janssens, 1940b. In addition, *Scarabaeolus* Balthasar, 1965a, was revalidated at subgeneric level.

Subsequent to 2005, nomenclature was, again, radically revised. Some taxa were revalidated as genera (*Pachysoma*; *Parateuchus* Shipp, 1895e) or raised to generic level (*Scarabaeolus*) (Forgie et al. 2006; Moretto 2016b). Some taxa were cited as subgenera (*Scarabaeus s. str.* Linnaeus, 1758), created as new subgenera (*Escarabaeus* Zídek & Pokorný, 2011; *Pachylosoma* Zídek & Pokorný, 2008) or revalidated as subgenera (*Mnematium*; *Ateuchetus* Bedel, 1892b) (Zídek & Pokorný 2008, 2011). Together with *Mnematidium* and *Kheper*, all of these subgenera were, thereafter, raised to generic status by Ziani and Gudenzi (2012), except for *Pachylosoma*. Thus, the tribe currently comprises ten genera (*Pachylomera*, *Kheper*, *Escarabaeus*, *Scarabaeus s. str.*, *Ateuchetus*, *Parateuchus*, *Scarabaeolus*, *Mnematium*; *Mnematidium*, *Pachysoma*) and two subgenera of *Scarabaeus s. str.* (*Pachylosoma*, *Sceliages*).

In the present work, we have followed the most recent rulings on status for each higher taxon (as of Nov. 2017) with one exception (*Sceliages* is treated as a genus). Thus, representatives of the tribe in South Africa, Botswana and Namibia are treated as seven genera. They are listed below in rank order of derivation according to Forgie et al. (2005), which suggests *Pachylomera* is more basal, *Pachysoma* more derived and the remainder, essentially, sister genera.

(1) *Pachylomera* Griffith & Pidgeon, 1831: Genus comprising two S Afrotropical species centred on deep sands, particularly, the Kalahari and outliers.

(2) *Kheper* Janssens, 1940b: An Afrotropical and Oriental genus including ten southern African species with widespread or restricted distributions centred in savanna (6), N upland grassland (1), SW Kalahari deep sand (1) SW winter rainfall region (1), NW arid late summer rainfall region (1)

(3) *Escarabaeus* Zídek & Pokorný, 2011: An Afrotropical and Palaearctic genus with two southern African species centred in the SW Arid late summer rainfall region or alluvial soils in the N Botswana Kalahari.

(4) *Sceliages* Westwood, 1837b: S Afrotropical genus with specialised breeding using millipede body contents; not yet formally revalidated at generic level; six species in South Africa and Botswana centred on winter and bimodal rainfall regions (2), Kalahari deep sand (1) or E savanna (3).

(5) *Scarabaeolus* Balthasar, 1965a: S Afrotropical centred genus comprising 27 South African, Botswanan and Namibian species with widespread or restricted distributions centred in the Namib Desert (4), winter and bimodal rainfall regions (2), Kalahari deep sands (9), SW Arid late summer rainfall region (5), E savanna (6), savanna and Karoo (1). However, further species were added by Zídek & Pokorný (2018) (see Preamble).

(6) *Scarabaeus s. str.* Linnaeus, 1758: Afrotropical, Palaearctic and W Oriental genus; revision required as the 31 or 33 South African, Botswanan and Namibian species would probably belong to several different genera in addition to *Scarabaeus s. str.* according to the principles of subdivision used by Ziani and Gudenzi (2012); species with widespread or restricted distributions centred in the Namib Desert (2), Kalahari deep sands (2), Kalahari and Namib Desert (2), winter and bimodal rainfall regions (7), Upper Karoo (1), upland grassland (8), savanna (10), E forest (1).

(7) *Pachysoma* Macleay, 1821: Flightless SW Afrotropical genus comprising 13 species endemic to the arid W coasts of South Africa and S Namibia.

Genus *Escarabaeus* Zídek & Pokorný, 2011

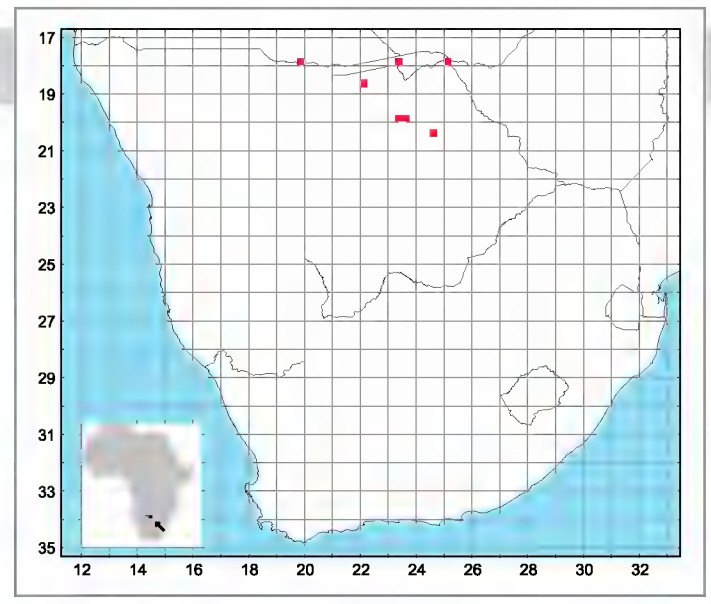
Type species and designation: *Scarabaeus cristatus* Fabricius, 1775, by original designation.
Synonyms: = *Mesoscarabaeus* Zídek & Pokorný, 2008: pre-occupied name; type species: *Scarabaeus cristatus* Fabricius, 1775, by original designation.
Last review: Formally created and reviewed as *Mesoscarabaeus* (Zídek & Pokorný 2008); renamed *Escarabaeus* with updated species list (Zídek & Pokorný 2011); raised to generic status (Ziani & Gudenzi 2012).

Escarabaeus Zídek & Pokorný, 2011, is a *nom nov.* for the pre-occupied, subgeneric name of *Mesoscarabaeus* Zídek & Pokorný, 2008, which has subsequently been raised to generic level (Ziani & Gudenzi 2012). It comprises eight confirmed species with combined distributions primarily in arid to dry areas of the Afrotropical, S Palaearctic and W Oriental regions.

Generic membership of Palaearctic species is supported by a clade in the morphological phylogeny of Barbero et al. (1998). Only two species from southern Africa are officially designated as members of the genus at present: *E. satyrus* (Boheman, 1857) and the recently described close relative, *E. remii* Davis & Deschodt, 2017. These two validated members of the genus in southern Africa show distributions centred on the arid SW and alluvial soils in N Botswana where habitat transformation is mostly limited. Therefore, both are assessed as Least Concern (LC).

Escarabaeus remii

Davis & Deschodt, 2017

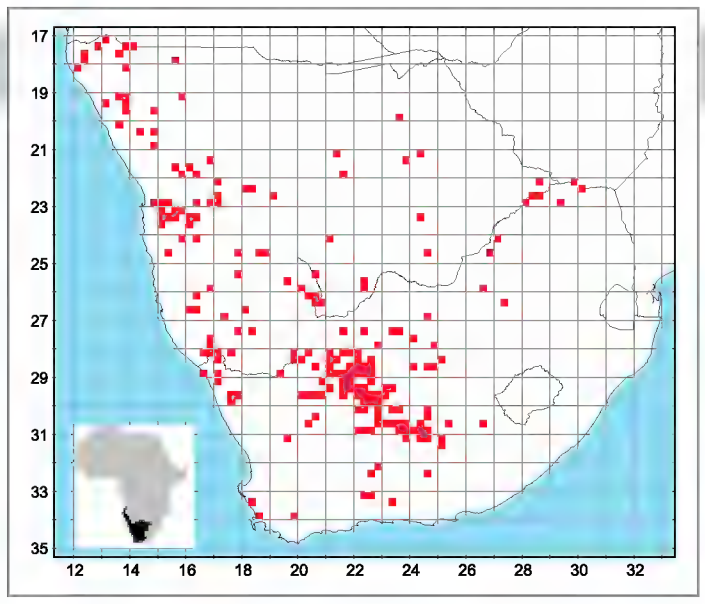


No synonyms

Global: LC
Endemic: Botswana, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Botswana, Okavango, Thamalakane riv.'.
Taxonomy: Accepted species; newly described, smaller-bodied, close relative of *Escarabaeus satyrus* (Boheman, 1860).
Distribution: Centred on alluvial soils of the Okavango Delta and Makgadikgadi Pan: N Botswana, NE Namibia.
Locality data (mean ± SD, range): Altitude: 937 ± 60, 871–1 075 m; annual rainfall: 503 ± 93, 399–647 mm; annual temperature (max. + min. /2): 22.4 ± 0.2, 22.1–22.7°C (N=9).
Habitat: No quantitative assessment; one DBRU collection record from grey sand in open mopane woodland.
Food types: No quantitative assessment; one DBRU collection record from cattle dung.
Temporal activity: Flight activity in darkness, primarily during the summer rainy season (Sept. to Mar.).
Ecoregions Namibia, Botswana: Primarily Zambezian Flooded Grasslands (AT0907), Zambezian Halophytics (AT0908) embedded within other ecoregions (see summary table).
Assessment rationale: EOO = 74 550 km^2; occupies a fairly large EOO in an area with a high degree of protection; unclear if AOO would be proportionately much smaller as ecologically poorly known; on basis of wide range and protection, currently assessed as Least Concern (LC).
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations and AOO; protected in Makgadikgadi Pans Game Reserve.



Escarabaeus satyrus

(Boheman, 1860)

= *Scarabaeus burchelli* Gillet, 1911

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Ateuchus satyrus*: 'juxta fluvios Svakop et Nolagi' [near Swakop River (W Namibia) and Nolagi, which is an untraced locality, possibly in Namibia or Botswana]; *S. burchelli*: 'tous d'Afrique australe' [all southern Africa].

Taxonomy: Accepted species; habitus close in appearance to *S. deludens* zur Strassen, 1961, but aedeagus differs radically.

Distribution: Arid to dry regions of SW Africa, often on sandy soils; SW Angola, Namibia, Botswana, South Africa; centred in the arid late summer rainfall region, also on Kalahari deep sands, present only as a rarity in the vicinity of Cape Town; record from Somalia considered an error due to interpretation of untraced type locality of 'Nolagi' as a misspelling of 'Nogali', Somalia; citations from Somalia and Ethiopia presumably errors.

Locality data (mean ± SD, range): Altitude: 1 017 ± 304, 1–2 074 m; annual rainfall: 230 ± 101, 22–655 mm; annual temperature (max. + min. /2): 18.2 ± 2.0, 12.9–23.3°C (N=342).

Habitat: No adequate quantitative assessment; in Northern Cape: most abundant in warm arid Bushmanland (3.3 per sample in 57 of 67 samples = 85.1%), but less abundant on deep Kalahari sands (1.1 in 64 of 98 = 65.3%), cooler uplands to S of Orange River (0.8 in 95 of 121 = 78.5%), and cool Upper Karoo (0.3 in 38 of 68 = 55.9%); DBRU collection records mainly from sandy soils: sand (20), sandy loam (4), sandy clay loam (1), in open vegetation, grassland (8), scrub/shrubland (12), open woodland (5).

Food types: No quantitative assessment; DBRU collection records from herbivore dung: cattle (16), horse (1), donkey (1), goat + sheep pellets (1).

Temporal activity: Flight activity during darkness in warmer months of the year across the mid-summer, late summer, winter and bimodal rainfall regions (Sept. to May); attracted to light.

Ecoregions Namibia, Botswana: Centred on arid ecoregions; Nama Karoo (AT1314), N Succulent Karoo (AT1322), Kaokoveld Desert (AT1310), Namib Desert (AT1315), Namibian Savanna Woodlands (AT1316), Kalahari Xeric Savanna (AT1309), marginal in three savanna ecoregions to NE.

Bioregions South Africa: Centred on Bushmanland (NKb), Upper Karoo (NKu) (Nama Karoo Biome); also Eastern Kalahari Bushveld (SVk), Kalahari Duneveld (SVkd) plus W margins of Central Bushveld (SVcb), Mopane (SVmp) (Savanna Biome); marginal in Succulent Karoo (SK) and Fynbos (F) biomes.

Assessment rationale: EOO = 1 491 750 km^2; widespread across an arid range used primarily for grazing of domestic livestock and conservation; high frequency of records in farm rangeland where it is readily attracted to herbivore dung of farm livestock; assessed as Least Concern (LC) owing to large, mostly little-transformed EOO.

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; protected in Kgalagadi Transfrontier Park (South Africa, Botswana), Namib-Naukluft and Etosha national parks (Namibia).

Genus *Kheper* Janssens, 1940b

Type species and designation: *Ateuchus aegyptiorum* Latreille, 1823, by original designation.
Synonyms: None.
Last review: Entire genus reviewed by Janssens (1940b); three new valid species described subsequently (Davis 1986; Deschodt et al. 2011; Pokorný & Zídek 2015), one revalidated from synonymy (Moretto 1998), and one transferred from *Scarabaeus* (present publication).

Kheper Janssens, 1940b, was described as a full genus. Although it was recently reduced to subgeneric status (Forgie et al. 2005), it has since been revalidated at generic level (Ziani & Gudenzi 2012). Furthermore, the most recently discovered new species (Pokorný & Zídek 2015) was described under *Kheper* at generic level. Unlike other members of the tribe Scarabaeini, some species show metallic colouration.

It currently comprises 25 valid, large-bodied species primarily characteristic of African savannas south of the Sahara (22 species), but also the W Oriental region (3 species: India, Sri Lanka) and margins of the Palaearctic region (Afghanistan). Exceptionally, of the 22 African species, three are found in arid and winter rainfall regions in the SW.

The genus is divisible into three species groups on the basis of the presence of two, one or no spines on the dorsal surface of the fore tibia at the base of tibial teeth 3 and/or 2 (Davis 1986). This may or may not parallel the three forms of the scutellum that have been noted for *Kheper*: shield-shaped, triangular or sub-triangular (Ziani & Gudenzi 2012).

A total of ten species occur within the study area in southern Africa including one species, *Scarabaeus vethi* (van Lansberge, 1886), here transferred to *Kheper*.

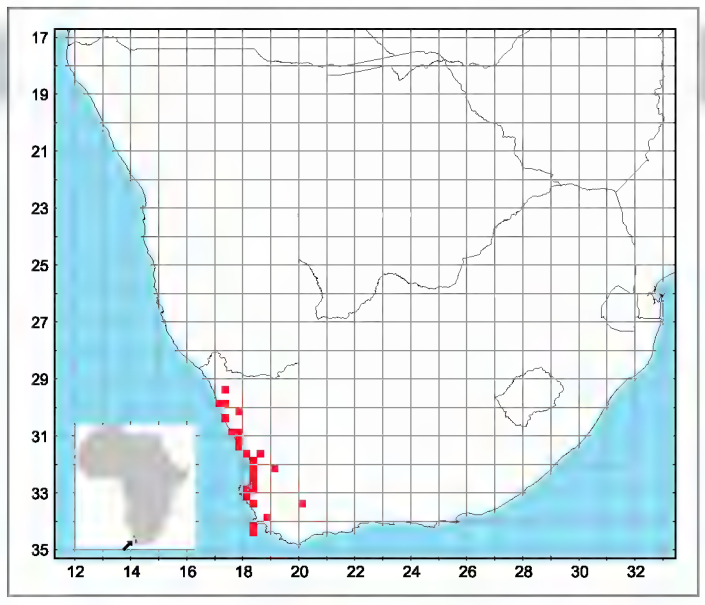
Group 1: Two spines on dorsal surface of protibiae; one each at the bases of tibial teeth 2 and 3. Comprises three species with distributions in all savanna (2 spp.) or E savanna only (1); all showing distributions into the tropics. Two showing associations with monogastric herbivore dung, one a night-flier.

Group 2: One spine on dorsal surface of protibiae at base of tibial tooth 2. Comprises six diurnal species with distributions in E savanna (1), Maputaland (1), N Highveld (1), W Cape coast (1), SW Kalahari (1), N Namibia coast (1).

Group 3: No spines on dorsal surface of protibiae at bases of tibial teeth. Comprises one night-flying species in savanna with a distribution into the tropics.

Grouping matches behaviour. In Group 1, pheromone may be released by males to attract females to a dropping. Also, balls intended for breeding are very large as 2–3 broods (or more) are constructed per breeding chamber. Group 2 roll smaller balls and may construct only a single brood per breeding chamber, which may explain why some species are able to survive in arid areas. If rolling in pairs, the female sits on the side of the ball rolled by the male. If rolled only by a male, he releases a pheromone at the burial site to attract a female. Females may breed once or twice a year raising breeding success by tending the brood during development of immatures. They are able to breed following a single rainfall event (refers *K. nigroaeneus* (Boheman, 1857): Edwards 1988; Edwards & Aschenborn 1988).

Seven species are currently assessed as Least Concern (LC) and three are Data Deficient (DD). However, clearance of natural shrubland in the Western Cape is a cause for concern (*K. bonellii* (Macleay, 1821)) as well as small range (700 km^2) in a highly transformed area of NE KwaZulu-Natal (*K. clericus* (Boheman, 1857)). Furthermore, *K. zurstrasseni* Davis, 1986, is known by only few museum specimens and has not been recorded since 1936.



Kheper bonellii

(Macleay, 1821)

No synonyms

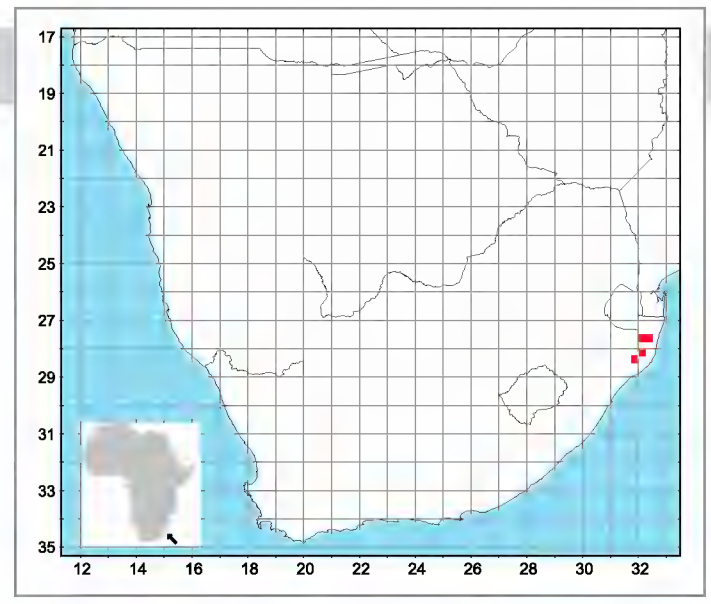
Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Scarabaeus bonellii*: 'Cap Bon. Spei' [Cape of Good Hope, South Africa].
Taxonomy: Accepted Group 2 species.
Distribution: Restricted to the winter rainfall region, South Africa, where it is centred on deep sands of the West Coast from the Cape Peninsula as far as the Richtersveld; a few in adjacent dry uplands.
Locality data (mean ± SD, range): Altitude: 162 ± 226, 0–975 m; annual rainfall: 223 ± 103, 88–429 mm; annual temperature (max. + min. /2): 17.1 ± 1.0, 15.7–18.5°C (N=36).
Habitat: In Western Cape: quantitative data inconclusive; abundant on deep sand in shrubland at Modderrivier (89); also in shrubland at Pampoenvlei on deep sand (13) or sandy loam (31) and on sandy soils in rough pasture at Oranjefontein (48); rare in sparse pasture at Groote Post (2) and Kikuyu pasture at Waylands (0); DBRU collection records primarily from deep sands (8) in natural scrub/shrubland (7); few records from sandy loam (2), sandy clay loam (1), or disturbed habitats, fallow crop fields (2), sparse pasture (1).
Food types: No quantitative assessment; DBRU collection records from the dung of cattle (10) and horse (2).
Temporal activity: Diurnal flight activity; in the Western Cape: narrow Aug. to Oct. peak in seasonal activity tailing off into Nov. and Dec.; tenerals only in Aug. and Sept. suggesting an annual breeding cycle with seasonal dormancy between spring activity peaks.
Bioregions South Africa: Centred on Namaqualand Sandveld (SKs) (Succulent Karoo Biome); W vegetation units in West Strandveld (FS), Sand Fynbos (FFd), Sandstone Fynbos (FFs) (Fynbos Biome).
Assessment rationale: EOO = 25 000 km^2; little threatened in N part of range that is used primarily for grazing of livestock, (transformation: 3–10%); assessment of threats from cultivation and urbanisation in southern range (transformation: 25–50% (FS), 40–55% (FFd), 75% (FFs)) not possible due to inconclusive quantitative results; currently assessed as Least Concern (LC) on basis of low transformation in N of range.
Conservation measures: Assessment of conservation status would be improved by additional quantitative data on ecological associations, particularly further assessment of threats due to vegetation transformation in the S; protected in West Coast National Park and the coastal part of Namaqua National Park; also Cape of Good Hope Nature Reserve and the private Grotto Bay Nature Reserve where it was frequently recorded in 1987 when the natural shrubland of the coastal strip was part of the Farm Modderrivier and was used for grazing cattle.

Kheper clericus

(Boheman, 1857)



No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Ateuchus clericus*: 'Caffraria interiore' [probably interior of SE South Africa].

Taxonomy: Accepted Group 2 species; type collected by J. Wahlberg; labelled 'Natal, Caffraria'.

Distribution: Localised on the narrow coastal plain in the Maputaland Centre of Endemism, KwaZulu-Natal, South Africa.

Locality data (mean ± SD, range): Altitude: 161 ± 81, 55–273 m; annual rainfall: 833 ± 85, 738–904 mm; annual temperature (max. + min. /2): 21.2 ± 0.6, 20.5–22.0°C (N=5).

Habitat: No adequate quantitative assessment; in uMkhuze Game Reserve, recorded only on clay (4), not on sandy clay loam, duplex soil (sand on sandy clay loam) or sand; DBRU collection records only from finer-grained soils (one each on clay, sandy clay loam, sandy loam) in savanna woodland (4).

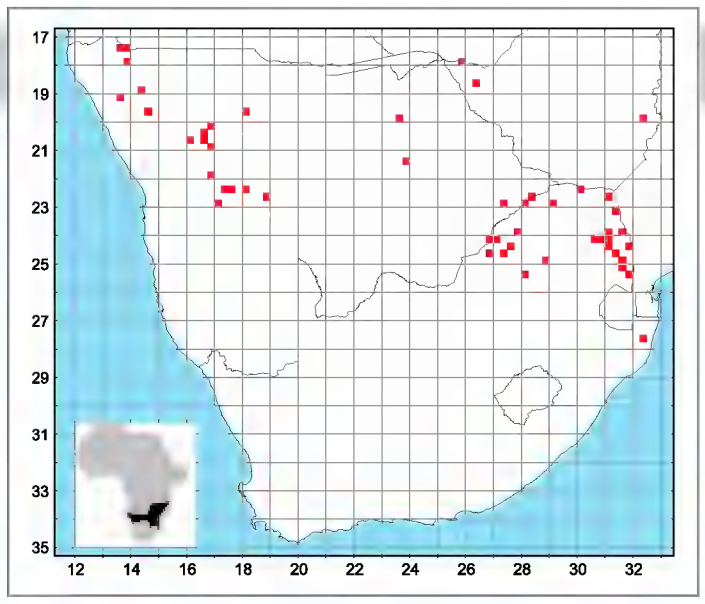
Food types: No quantitative assessment; DBRU collection records from the dung of square-lipped (white) rhinoceros (1) and zebra (1).

Temporal activity: Diurnal flight activity in early summer (Oct. to Dec.).

Bioregions South Africa: Vegetation units: Zululand Lowveld (SVl 23), Western Maputaland Clay Bushveld (SVl 20) (SE extremity of Lowveld (SVl), Savanna Biome).

Assessment rationale: EOO = 750 km^2; collection records exclusively on finer-grained soils and monogastric herbivore dung in wooded areas of game reserves are too limited to draw clear conclusions, therefore, currently assessed as Data Deficient (DD); however, possible specialisation and restricted known occurrence within a very small range may warrant allotment of a threat category of at least Vulnerable (VU); although habitat transformation by cultivation is 26–34% in SVl 20 and SVl 23, possible effect of woodland loss is unknown.

Conservation measures: Owing to limited information, assessment of conservation status would be improved by further quantitative data on soil, dung and vegetation associations both within and outside of reserves on the coastal plain; protected in uMkhuze and Hluhluwe–iMfolozi game reserves.



Kheper cupreus

(Castelnau, 1840)

= *Ateuchus aeruginosus* Klug, 1855
= *Ateuchus metallicus* Boheman, 1857
= *Kheper namibicus* Krajcik, 2006

Global: LC (see IUCN Red List – LC as *Scarabaeus namibicus*)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Ateuchus cupreus*: 'Caffrerie' [probably South Africa]; *A. aeruginosus*: 'Tette' [Tete, central Mozambique]. *A. metallicus*: 'in tractus fluvii Limpoponis' [Limpopo River course, southern Africa]; *K. namibicus*: 'NAMIBIA, road C20 10 km S of Gobabis'.

Taxonomy: Accepted Group 3 species; colour variation from black with iridescent sheen to iridescent cupreous.

Distribution: Centred on hot, dry savanna in southern central Africa: N South Africa, Botswana, N Namibia, Zimbabwe; also reported from Mozambique, S Democratic Republic of the Congo (DRC) and S Tanzania.

Locality data (mean ± SD, range): Altitude: 866 ± 465, 55–1 924 m; annual rainfall: 487 ± 134, 171–743 mm; annual temperature (max. + min. /2): 21.0 ± 1.8, 16.8–25.9°C (N=59).

Habitat: No adequate quantitative assessment; DBRU collection records shared between sand (5), sandy loam (4) and sandy clay loam (1), primarily in shrub/woodland (8), rare in grassland (1).

Food types: At Phalaborwa, attracted to small baits of pig (9) or cattle (9) dung, but not elephant (0); DBRU collection records from dung of cattle (9), hook-lipped (black) rhinoceros (1) and wildebeest (1).

Temporal activity: Flight activity in darkness as indicated by tan-coloured pilosity; mid-summer activity from Nov. to Feb.; at Phalaborwa: more abundant immediately following substantial rainfall (15) compared to drier conditions (2); attracted to light.

Ecoregions Namibia, Botswana, Zimbabwe: N Namibia Savanna Woodlands (AT1316), Kalahari Xeric Savanna (AT1309), Kalahari Acacia-Baikiaea Woodlands (AT0709), Angolan Mopane Woodlands (AT0702), Zambezian and Mopane Woodlands (AT0725), Southern African Bushveld (AT0717).

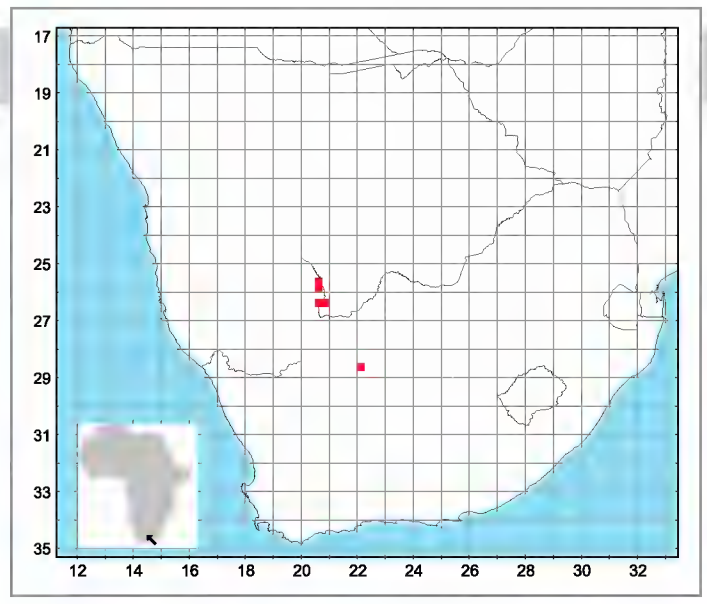
Bioregions South Africa: Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 1 865 025 km^2; widespread on various soil types in dry savannas of southern central Africa within both game reserves and farmland as it is readily attracted to the dung of both omnivores and ruminant herbivores; assessed as Least Concern (LC), although a possible association with woodland savanna would render it susceptible to habitat transformation, which stands at 0–58% (SVl), 2–49% (SVcb) or 0–20% (SVmp) across the South African part of its range.

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, particularly vegetation associations; protected in various South African nature reserves including the Kruger National Park plus Hwange National Park, Zimbabwe.

Kheper kalaharicus

(Davis, Deschodt & Scholtz, 2011)

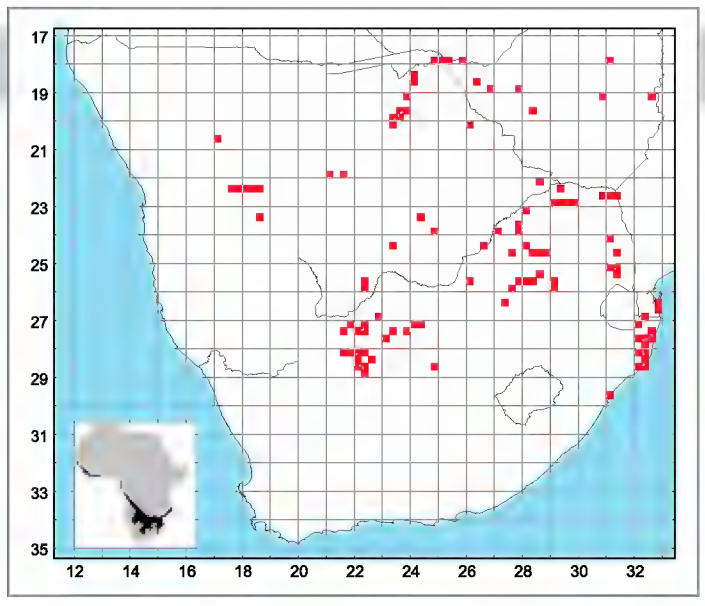


No synonyms

Global: LC
Endemic: RSA, Botswana

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Scarabaeus* (*Kheper*) *kalaharicus*: 'Kgalagadi Transfrontier Park' [Botswana].
Taxonomy: Accepted Group 2 species.
Distribution: Probably restricted to the SW Kalahari dune field straddling the borders of Namibia, Botswana and South Africa.
Locality data (mean ± SD, range): Altitude: 953 ± 85, 908–1 124 m; annual rainfall: 209 ± 19, 188–239 mm; annual temperature (max. + min. /2): 20.4 ± 0.8, 19.0–21.1°C (N=6).
Habitat: No quantitative data, but all specimens (45) sampled from shrub/grassland on arid deep sands of a dune field, an association that may account for the elongate body shape.
Food types: In Botswana: not attracted to carrion, but shows a very strong bias to pig dung with much lower attraction to other dung types: carrion (0), pig (31), elephant (1), cattle (3), sheep dung (8).
Temporal activity: Diel periodicity not known, but presumably diurnal flight as indicated by black pilosity; active during the late summer rainy season (Feb., Mar.).
Ecoregions Botswana: Kalahari Xeric Savanna (AT1309).
Bioregions South Africa: Kalahari Duneveld (SKvd) (Savanna Biome).
Assessment rationale: EOO = 6 000 km^2; undoubtedly underestimated; probably faces few threats in a dune field that is used primarily for grazing domestic livestock or is under conservation; assessed as Least Concern (LC).
Conservation measures: Assessment of conservation status would be improved by quantitative data to confirm habitat associations; protected in Kgalagadi Transfrontier Park (Botswana and South Africa).



Kheper lamarcki

(Macleay, 1821)

= *Ateuchus infernalis* Klug, 1855

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Scarabaeus lamarckii*: 'Senegallia' [Senegal]; *A. infernalis*: 'In Mossambique verbreitet, eben so, gewöhnlich kleiner, in Port Natal' [evenly distributed in Mozambique, usually localised in Durban, South Africa].

Taxonomy: Accepted Group 1 species.

Distribution: Widespread, but localised on deep sands in hot, dry savanna from W to S central and southern Africa; mega-Kalahari, E coast and intervening sand outliers: South Africa, Botswana, Namibia, Zimbabwe, Mozambique, Angola, Democratic Republic of the Congo (DRC) and Senegal; also reported from Guinea (Conakry).

Locality data (mean ± SD, range): Altitude: 849 ± 454, 0–1 628 m; annual rainfall: 548 ± 218, 220–1 275 mm; annual temperature (max. + min. /2): 20.7 ± 1.6, 16.1–25.2°C (N=153).

Habitat: In Gauteng: exclusively on coarse-grained soils, deep sand (261), sandy clay loam (0) with a bias to wooded savanna, grassland (48), open woodland (170), shaded thickets (43); in uMkhuze Game Reserve: equally strong bias to coarse-grained soils, sand (8.8), duplex soils (sand over clay) (2.0), sandy clay loam (0.0), clay (0.5); largely supported by DBRU collection records: sand (29), sandy loam (14), sandy clay loam (1) in grassland (12) or shrub/woodland (31).

Food types: In both Gauteng and Botswana: strong bias to omnivore dung; in Gauteng bushveld: carrion (0), pig (69), horse (4), cattle dung (9); in Botswana: carrion (115), pig (3 336), elephant (996), cattle (576), sheep dung (484); DBRU collection records on various dung types: cattle (35), buffalo (1), wildebeest (1), elephant (5), square-lipped (white) rhinoceros (1), horse (1), waterbuck (1).

Temporal activity: Diurnal flight activity in both sunny and cloudy conditions as long as temperatures are sufficiently high; in Gauteng bushveld: active in the summer rainy season (Oct. to Apr.), also May, Aug. and Sept. on the warmer E coastline.

Ecoregions Namibia, Botswana, Zimbabwe, Mozambique: Deep sands: Kalahari Xeric Savanna (AT1322), Kalahari Acacia-Baikiaea Woodlands (AT0709), Southern African Bushveld (AT0717), Zambezian and Mopane Woodlands (AT0725), Maputaland Coastal Forest Mosaic (AT0119).

Bioregions South Africa: Deep sands in E Kalahari Duneveld (SVkd), Eastern Kalahari Bushveld (SVk), Central Bushveld (SVcb), Mopane (SVmp), Lowland (SVl) (Savanna Biome); also Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 2 173 065 km^2; widespread on deep sands in both farm rangeland and conserved areas as it is readily attracted to a range of dung types despite a bias to omnivore dung; vegetation bias suggests that clearance of woodland would result in a fourfold reduction in population density; in South Africa, transformation low in W vegetation units of SVk (0–2%), but often higher in SVcb, SVmp and SVl (0–58%); assessed as Least Concern (LC) on basis of high frequency across a wide range.

Conservation measures: None recommended; protected in various reserves containing deep sands, including uMkhuze Game Reserve, Kruger National Park and iSimangaliso Wetland Park (World Heritage Site) (South Africa), Chobe National Park (Botswana) and Maputo Special Reserve (Mozambique).

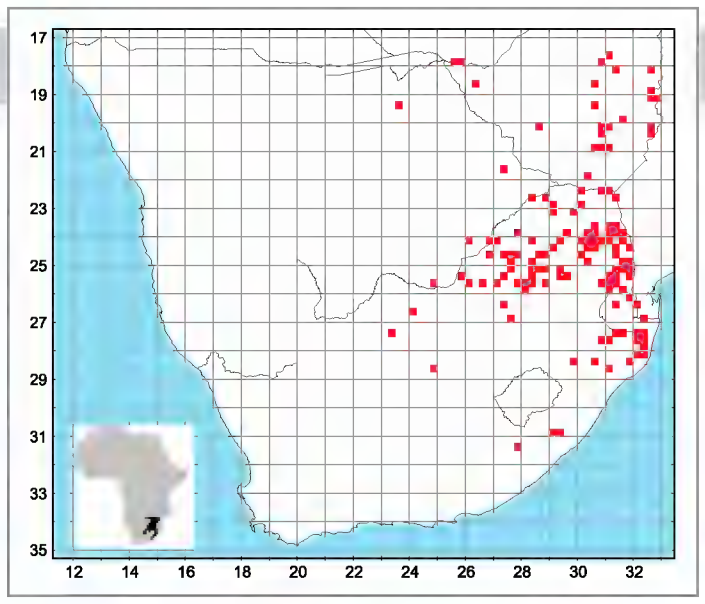
Kheper nigroaeneus

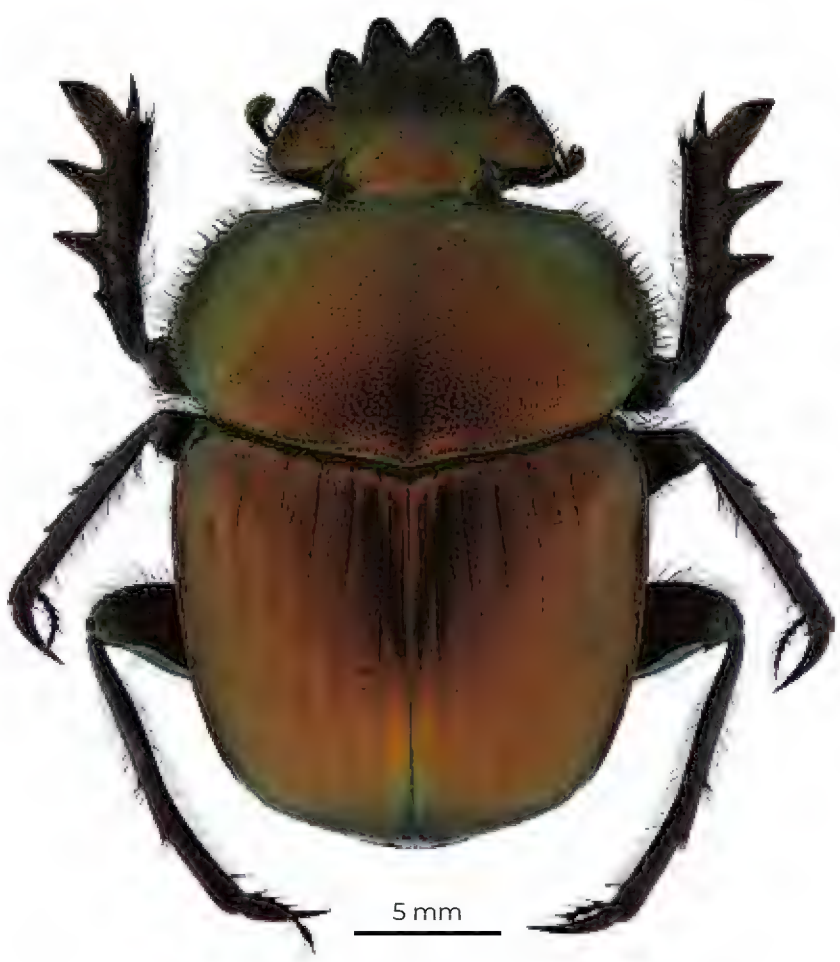
(Boheman, 1857)

= *Scarabaeus usurpator* Péringuey, 1901

Global: LC (see IUCN Red List – LC as *Scarabaeus*)

J	A	S	O	N	D	J	F	M	A	M	J





Type localities: As *Ateuchus nigroaeneus*: 'Caffraria interiore' [interior of SE South Africa]; *S. usurpator*: 'Manica, Mozambique'.

Taxonomy: Accepted Group 2 species; colour variation from black to iridescent cupreous; green iridescence in some black individuals.

Distribution: Centred on hot, dry to moist savanna in E southern Africa: N South Africa, E Botswana, Zimbabwe, Mozambique; Namibian record requires validation.

Locality data (mean ± SD, range): Altitude: 840 ± 433, 1–1 670 m; annual rainfall: 672 ± 158, 306–1 415 mm; annual temperature (max. + min. /2): 20.1 ± 2.0, 14.2–25.2°C (N=207).

Habitat: In uMkhuze Game Reserve: no clear soil type bias, sand (31.7), duplex soil (sand over clay) (27.6), sandy clay loam (46.6), clay (8.8); no quantitative assessment of vegetation association; DBRU collection records from sand (10), sandy loam (19), sandy clay loam (13), clay (0) in pasture/grassland (13), shrub/woodland (25) and thickets/forest (2).

Food types: At Phalaborwa: clear bias to omnivore dung (pig, 736; cattle, 406; elephant, 144), although prominent on fresh elephant droppings in the Kruger National Park; DBRU collection records from dead cricket (1) and various dung types: baboon (1), elephant (2), rhinoceros (3), donkey (1), cattle (32), buffalo (2), wildebeest (2), waterbuck (1).

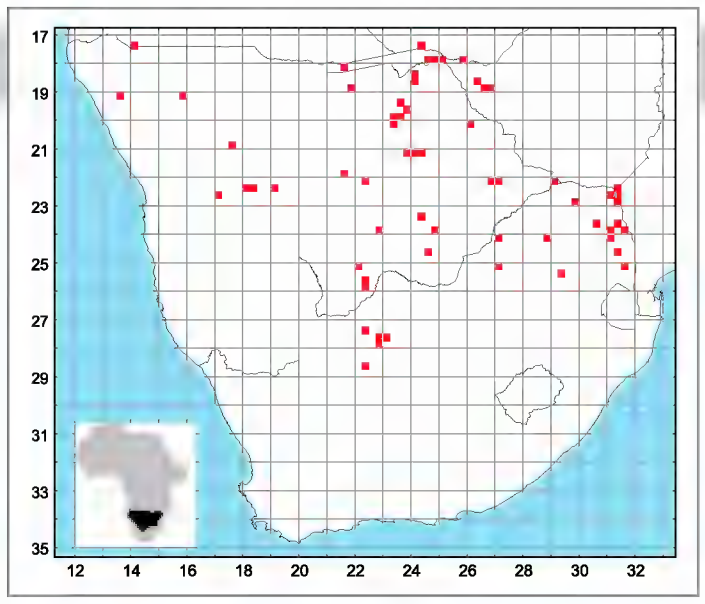
Temporal activity: Diurnal flight activity, especially in the cooler early morning during the summer rainy season (mainly Oct. to Apr.); ball intended for breeding is rolled by male on his own or with female clinging to the side; if alone, male releases pheromone at burial site to attract female; females tend a single brood in a chamber in the soil from early in the seasonal activity period; tenerals appear in Mar. (Edwards 1988); females may or may not breed again and tend a brood during winter; at Phalaborwa: much greater activity in warm conditions after heavy rainfall (981) compared to hot, dry (190) or warm cloudy conditions after light rainfall (110).

Ecoregions Botswana, Zimbabwe: Centred on Southern Miombo Woodlands (AT0719), Southern African Bushveld (AT0717), marginal in moister parts of Zambezian and Mopane Woodlands (AT0725), E Kalahari Xeric Savanna (AT1309), E Kalahari Acacia-Baikiaea Woodlands (AT0709).

Bioregions South Africa: Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome); also sporadically in East Kalahari Bushveld (SVkb) (Savanna Biome) plus Sub-Escarpment Grassland (Gs) (Grassland Biome).

Assessment rationale: EOO = 662 125 km^2; widely distributed in both farm rangeland and conserved areas; recorded on a range of soil and dung types in both grassland and the open woodland that dominates its range; transformation in South Africa by cultivation and urbanisation (0–58% (SVl), 2–49% (SVcb) or 0–20% (SVmp)) would presumably be detrimental; however, assessed as Least Concern (LC) because of its abundance in the partially protected NE lowlands of South Africa.

Conservation measures: Assessment of conservation status would be improved by quantitative data on soil and vegetation associations; protected in various reserves including, uMkhuze and Hluhluwe–iMfolozi game reserves and Kruger National Park (South Africa).



Kheper prodigiosus

(Erichson, 1843)

= *Scarabaeus pubiventris* van Lansberge, 1874b

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Ateuchus prodigiosus*: Not stated; *S. pubiventris*: 'Mozambique'.

Taxonomy: Accepted Group 1 species.

Distribution: Widespread in hot, dry savanna; primarily on deep sands, of the summer rainfall region in southern central Africa: N South Africa, Botswana, Namibia, Angola, Zimbabwe, Zambia, Mozambique; Democratic Republic of the Congo (DRC), Tanzania records require validation.

Locality data (mean ± SD, range): Altitude: 891 ± 352, 102–1 730 m; annual rainfall: 484 ± 136, 171–813 mm; annual temperature (max. + min. /2): 21.3 ± 1.7, 16.8–25.9°C (N=76).

Habitat: No adequate quantitative assessment; on deep sands in Chobe National Park, Botswana: more abundant in grassland with trees (113) than open woodland (35) or dense woodland (33); DBRU collection records biased to sand (8), also sandy loam (3) in grassland (4) and open woodland (6).

Food types: In Botswana: bias to monogastric herbivore and omnivore dung: carrion (2), pig (62), elephant (143), cattle (26), sheep dung (18); DBRU collection records from dung of elephant (6), cattle (6), warthog (1).

Temporal activity: Flight activity in darkness during the summer rainy season (Nov. to May) as suggested by tan pilosity; attracted to light.

Ecoregions Namibia, Botswana, Zimbabwe: Centred on sandy soils in Kalahari Xeric Savanna (AT1309), Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian and Mopane Woodlands (AT0725), also Angolan Mopane Woodlands (AT0702) and margins of three other ecoregions.

Bioregions South Africa: Sandy areas of Eastern Kalahari Bushveld (SVk), Central Bushveld (SVcb), Mopane (SVmp) (Savanna Biome).

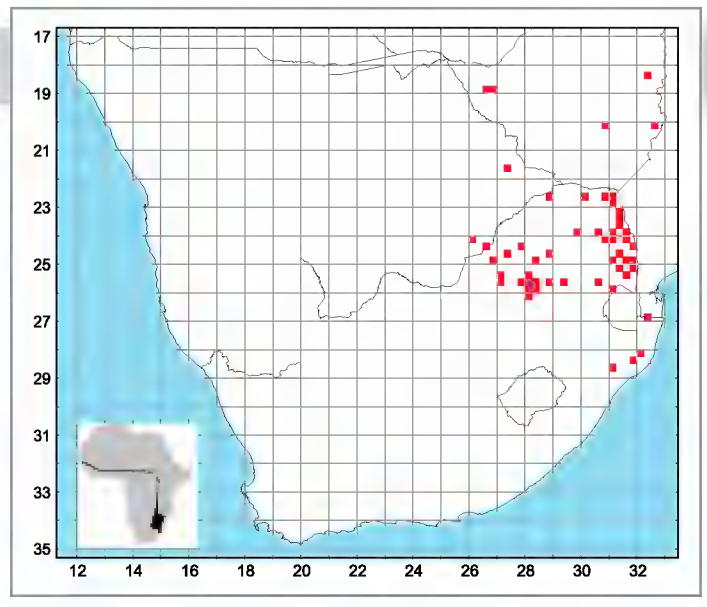
Assessment rationale: EOO = 2 045 625 km^2 (possibly underestimated); widespread although AOO presumably influenced by soil, vegetation and dung type bias; abundant on deep sands in NW Botswana where elephants are abundant (249), rare in the arid SW where elephants are absent (2); many collection records from game reserves, therefore, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on soil and vegetation associations as observations suggest these would be influential to AOO; protected in various national parks where elephants are conserved, including Kruger (South Africa), Chobe (Botswana), Etosha (Namibia), Hwange (Zimbabwe).

Kheper subaeneus

(Harold, 1869b)

= *Ateuchus lamarcki* Macleay, 1821, *sensu* Castelnau, 1840
= *Scarabaeus metallicus* Boheman, 1857, *sensu* Péringuey, 1901
= *Scarabaeus subaeneus* var. *orientalis* Gillet, 1907
= *Scarabaeus subaeneus* var. *atratus* Gillet, 1911
= *Kheper subaeneus angolensis* Janssens, 1940b



Global: LC (see IUCN Red List – LC as *Scarabaeus*)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Scarabaeus subaeneus*: 'Senegal'; as *A. lamarckii sensu* Castelnau: 'Senegal'; *S. metallicus sensu* Péringuey: 'Zambesia (Victoria Falls)' [Zimbabwe]; *S. subaeneus orientalis*: 'Mozambique'; *S. subaeneus atratus*: 'l'Oubangui et de la Chari' [Central African Republic (CAR)]; *K. subaeneus angolensis*: 'Angola'.

Taxonomy: Accepted Group 1 species; colour variation from black to iridescent cupreous.

Distribution: Widespread in hot, dry to moist savannas in southern, southern central, E central and W Africa; possibly localised by soil specialisation; validated for South Africa, Botswana, Zimbabwe, Mozambique, Angola; synonyms in CAR, Senegal; also reported from Democratic Republic of the Congo (DRC), Côte d'Ivoire, Ghana, Mauritania; possibly also Uganda, South Sudan.

Locality data (mean ± SD, range): Altitude: 750 ± 464, 55–1 635 m; annual rainfall: 641 ± 137, 317–1 177 mm; annual temperature (max. + min. /2): 20.8 ± 2.4, 16.3–25.9°C (N=88).

Habitat: No adequate quantitative assessment; DBRU collection records indicate a bias to finer-grained soils: sand (3), sandy loam (9), sandy clay loam (6) with similar numbers of records from pasture/grassland (7) and open woodland (7), also in forest (1).

Food types: At Phalaborwa: clear bias to dung of omnivores (pig, 60; elephant, 3; cattle, 4), but prominent on fresh elephant and rhinoceros droppings in game reserves; this bias is supported by DBRU collection records for elephant (16), rhinoceros (3) and buffalo dung (1) in reserves compared to cattle (7) and donkey dung (2) in farmland.

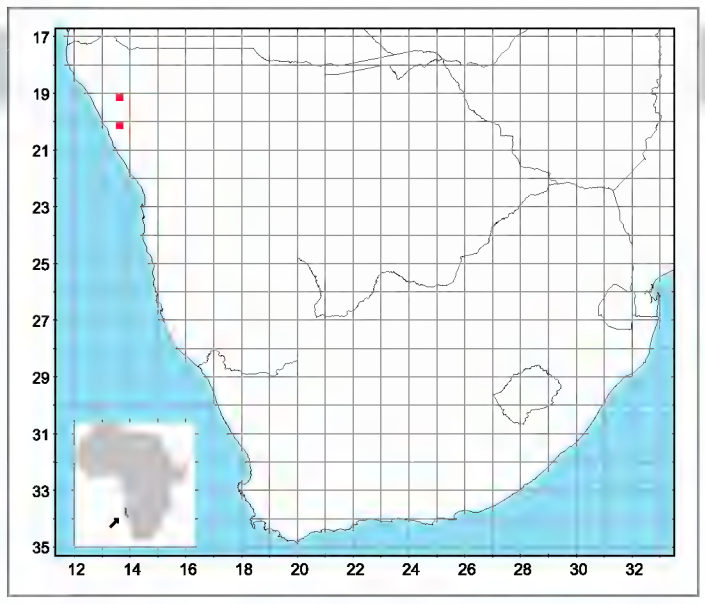
Temporal activity: Diurnal flight activity during the summer rainy season (Oct. to Apr.); at Phalaborwa: activity much greater in warm conditions after substantial rainfall (58) compared to hot, dry conditions (6) or warm cloudy conditions after light rainfall (0).

Ecoregions Botswana, Zimbabwe: E Kalahari Acacia-Baikiaea Woodlands (AT0709), Southern African Bushveld (AT0717), Zambezian and Mopane Woodlands (AT0725), Zambezian Baikiaea Woodlands (AT0726), Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 1 257 850 km^2 (probably underestimated); extremely widespread, but may be localised on finer-grained soils with greater population density in reserves that protect elephants and rhinoceros although this is not supported near the South African Wildlife College in the Kruger National Park (3.0) compared to adjoining farm rangeland (17.8); assessed as Least Concern (LC) owing to widespread occurrence and large number of records from reserves (61 out of 103).

Conservation measures: Assessment of conservation status would be improved by quantitative data on habitat and dung type associations both inside and outside of reserves that protect large monogastric herbivores on finer-grained soils; protected especially in the Kruger National Park and game reserves including Hluhluwe–iMfolozi, Roodeplaat (South Africa) and Lake Mutirikwe (Zimbabwe).



Kheper vethi

(van Lansberge, 1886)

No synonyms

Global: DD

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Scarabaeus vethi*: 'Benguela' [Angola].

Taxonomy: Accepted species, but here transferred to *Kheper* from *Scarabaeus*; classified in Group 2; identification of Kaokoveld specimens as *K. vethi* requires validation.

Distribution: Arid to dry coastal plain: N Namibia, SW Angola.

Locality data (mean ± SD, range): Altitude: 519 ± 224, 361–677 m; annual rainfall: 193 ± 37, 167–219 mm; annual temperature (max. + min. /2): 16.9 ± 0.3, 16.7–17.2°C (N=2).

Habitat: Not known.

Food types: Not known.

Temporal activity: Diel flight periodicity unknown, but presumably diurnal flight based on black pilosity; seasonal activity recorded during the late summer rainy season (Dec. to Feb.).

Ecoregions Namibia: On the border of the arid Kaokoveld Desert (AT1310) and N Namibian Savanna Woodlands (AT1316).

Assessment rationale: EOO = 35 400 km^2 (estimated); rarity may or may not be a collection artefact; two N Namibian localities lie outside the boundary of the Skeleton Coast Park and the Tora Conservancy although they do lie in an arid area used primarily for grazing of livestock; currently assessed as Data Deficient (DD).

Conservation measures: Current data is insufficient to determine conservation status; a survey needs to be conducted in N Namibia and particularly Iona National Park northwards to Benguela, SW Angola; not currently known from any officially protected area.

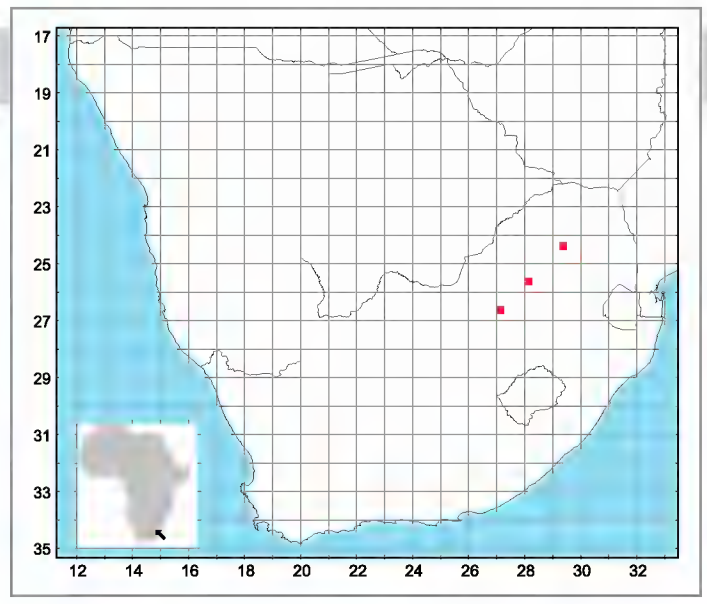
Kheper zurstrasseni

Davis, 1986

No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: 'Transvaal, Pretoria' [Gauteng, South Africa].
Taxonomy: Accepted Group 2 species.
Distribution: Locality records only from uplands in North-West, Gauteng and Limpopo provinces, South Africa.
Locality data (mean ± SD, range): Altitude: 1 206 ± 196, 1 013–1 356 m; annual rainfall: 626 ± 43, 588–672 mm; annual temperature (max. + min. /2): 18.2 ± 1.0, 17.3–19.2°C (N=3).
Habitat: Unknown.
Food types: Unknown.
Temporal activity: Diel flight periodicity unknown, but presumably diurnal based on black pilosity; a single temporal record in the summer rainy season (Feb.).
Bioregions South Africa: Difficult to assess; localities coincide with Mesic Highveld Grassland (Gm) (Grassland Biome) or lie close to patches of the same grassland type isolated in the adjoining Central Bushveld (SVcb) (Savanna Biome).
Assessment rationale: EOO = 1 450 km^2, probably underestimated, based on only three known localities; very poorly represented by only six specimens in the type series despite a distribution centred in an intensively sampled region; available data suggest it is highly threatened as the last known dated collection was made in 1936; qualifies for Endangered (EN) status on basis of EOO < 5 000 km^2 at < five localities, but is currently assessed as Data Deficient (DD).
Conservation measures: In view of its rarity in collections, *K. zurstrasseni* could be a relative specialist; however, as nothing is known of its habits, a range of habitat and dung types needs to be tested for its occurrence, starting around the three known, but relatively inexact localities, none of the known localities coincide with protected areas.

Genus *Pachylomera* Griffith & Pidgeon, 1831

Type species and designation: *Scarabaeus femoralis* Kirby, 1828, by monotypy.
Synonym: = *Pachylomerus* Bertolini, 1849: Type species: *Scarabaeus femoralis* Kirby, 1828, by monotypy.
Last review: Genus: Ziani & Branco (2011); Species: Janssens (1940b).

Although this genus has been long accepted as comprising only two species described in the 19th century, there has been much confusion over the validity of two available generic names (*Pachylomerus* or *Pachylomera*) and their authorship (Kirby 1828; Hope 1832 (unpublished); Bertolini 1849). A recent consideration of the complicated published history (Ziani & Branco 2011) has shown that none of the previous combinations is correct and that the valid name and authorship is *Pachylomera* Griffith & Pidgeon, 1831.

The genus shows a widespread EOO in the summer rainfall region of southern and S central Africa. Its AOO is much more restricted as it is centred on deep sands, particularly the mega-Kalahari from South Africa northwestwards to W Democratic Republic of the Congo (DRC), as well as deep sand outliers and coastal sands in the E from South Africa, reportedly as far N as coastal Tanzania. As both species are either centred on or restricted to Kalahari sands, neither is seriously threatened by habitat transformation although one species also occurs in areas of greater transformation.

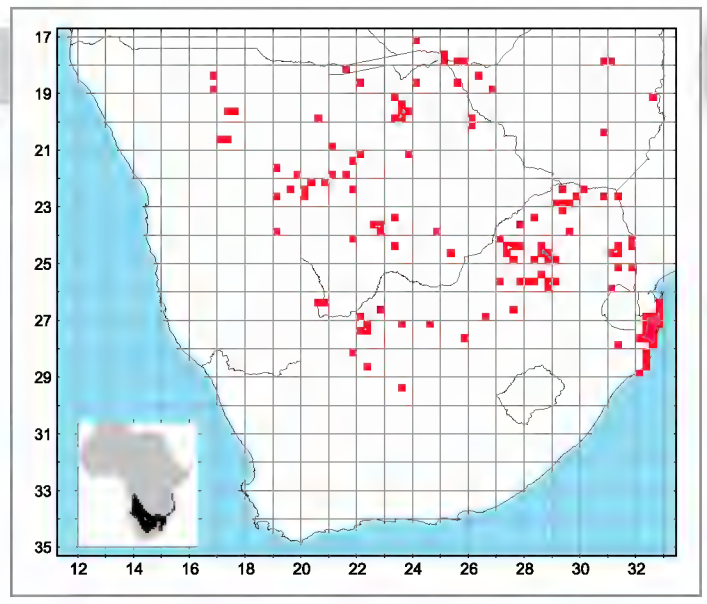
Pachylomera femoralis

(Kirby, 1828)

= *Ateuchus* (*Pachylomera*) *horridus* Boheman, 1857

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: As *Scarabaeus femoralis*: 'Soudan' [presumably an error; never since found in Sudan]; *A. horridus*: 'juxta fluvium Limpopo' [near Limpopo River, southern Africa].

Taxonomy: Accepted species; see discussion of generic name on genus page.

Distribution: Centred on moister deep sands of the mega-Kalahari and its outliers from South Africa across Botswana, Namibia, Zimbabwe, SW Zambia, Angola to W Democratic Republic of the Congo (DRC); also deep sands on E seaboard from South Africa across Mozambique to Tanzania.

Locality data (mean ± SD, range): Altitude: 796 ± 481, 0–1 696 m; annual rainfall: 583 ± 217, 194–1 270 mm; annual temperature (max. + min. /2): 20.9 ± 1.7, 16.6–25.5°C (N=197).

Habitat: In Gauteng bushveld: recorded exclusively on deep sand (70), absent from sandy clay loam (0); equally abundant in grassland (30) and open woodland (37) rare in shaded thickets (3); in uMkhuze Game Reserve: similar soil bias: deep sand (208.7), duplex soil (sand over clay) (22.2), sandy clay loam (0.3), clay (0.4); supported by DBRU collection records: sand (17), sandy loam (6), sandy clay loam (1) in grassland (9), shrubland (10), open woodland (8), forest (1).

Food types: In Botswana: bias to omnivore dung (pig: 5 131), but also abundant on carrion (1 149) and herbivore dung (elephant: 759, cattle: 607, sheep: 1 303); similar bias in Gauteng bushveld: (carrion: 3, pig: 15, horse: 2, cattle dung: 4); DBRU records from various dung types: elephant (3), horse (1), donkey (2), cattle (16), buffalo (1), wildebeest (1).

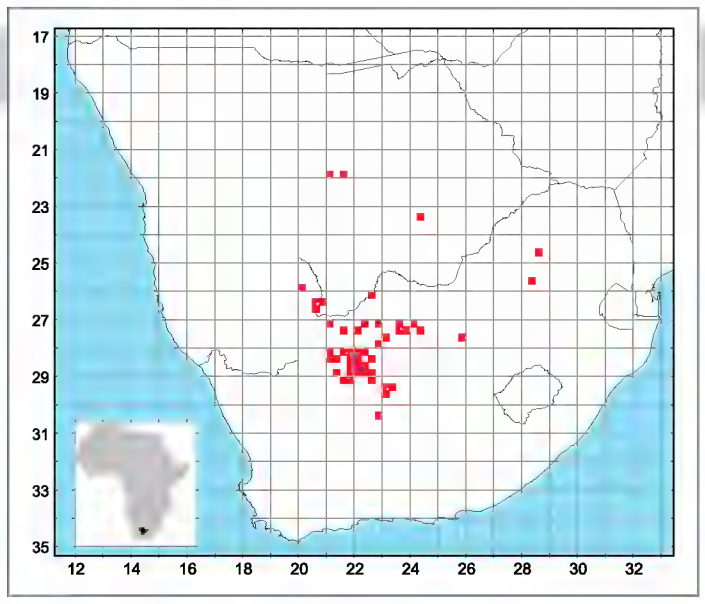
Temporal activity: Diurnal flight activity, even under cloudy conditions as long as temperatures are sufficiently high; in Gauteng bushveld: seasonal activity Oct. to Apr.; at least Aug. to May on warmer E coastline.

Ecoregions Namibia, Botswana, Zimbabwe, Mozambique: Deep sands, particularly in Kalahari Xeric Savanna (AT1309), Kalahari Acacia-Baikiaea Woodlands (AT0709), Angolan Mopane Woodlands (AT0702), Zambezian Baikiaea Woodlands (AT0726), Southern African Bushveld (AT0717), Zambezian and Mopane Woodlands (AT0725), Maputaland Coastal Forest Mosaic (AT0119).

Bioregions South Africa: Deep sands of Eastern Kalahari Bushveld (SVk), Central Bushveld (Svcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome); also Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 2 663 660 km^2; AOO restricted by the distribution of deep sands, but widespread in farm rangeland although vegetation units in NE part of South African range are subject to 0–58% transformation; *circa* 20% of southern African range protected in national parks and game reserves, therefore, assessed as Least Concern (LC).

Conservation measures: None recommended; widespread on deep sands in farm rangeland and protected in various national parks and game reserves, especially Chobe, Khutse (Botswana); Kruger, Hluhluwe–iMfolozi, Tswalu Kalahari (South Africa).



Pachylomera opaca

van Lansberge, 1874b

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Lac N'gami' [Lake Ngami, Botswana].

Taxonomy: Accepted species; see discussion of generic name on genus page.

Distribution: Centred on the arid southwest Kalahari deep sands; rare occurrence in mainland Kalahari sands: N Botswana, SW Zambia; however, also occurs in cooler deep sand outliers of Gauteng and Limpopo provinces, South Africa.

Locality data (mean ± SD, range): Altitude: 1 076 ± 151, 776–1 401 m; annual rainfall: 275 ± 91, 172–636 mm; annual temperature (max. + min. /2): 19.3 ± 0.9, 17.6–21.2°C (N=78).

Habitat: No quantitative assessment; DBRU collection records exclusively on deep sand (19) in pasture/grassland (9), scrub (3) or open shrubland (8); most records from arid localities, but occurs as a rarity at moister localities supporting open grassland.

Food types: In Botswana: attracted primarily to omnivore dung (pig: 28) less commonly to herbivore dung (elephant: 3, cattle: 1, sheep: 6); DBRU collection records on dung of cattle (12), horse (2), donkey (2).

Temporal activity: Diurnal flight activity during the summer rainy season (Oct. to Apr.).

Ecoregions Botswana: Scattered localities in Kalahari Acacia-Baikiaea Woodlands (AT0709).

Bioregions South Africa: Eastern Kalahari Bushveld (SVk), Kalahari Duneveld (SVkd) (Savanna Biome); N limits of Bushmanland (NKb), Upper Karoo (NKu) (Nama Karoo Biome); sand outliers in Central Bushveld (SVcb) (Savanna Biome).

Assessment rationale: Full EOO = 800 000 km^2; SW Kalahari EOO = 120 000 km^2; widespread, although AOO is limited by distribution of deep sand and open vegetation; not abundant on dung of domestic herbivore livestock, but frequently recorded on farms in the SW Kalahari in an area subject to only 0–2% transformation (W SVk); assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by by quantitative data on habitat associations; *circa* 10% of the SW Kalahari range protected within Kgalagadi Transfrontier Park (South Africa and Botswana); also protected in Telperion Nature Reserve (Gauteng in South Africa).

Genus *Pachysoma* Macleay, 1821

Type species and designation: *Pachysoma hippocrates* Macleay, 1821, by original designation.
Synonyms: = *Irrorhotides* Shipp, 1896a: Type species: *Irrorhotides fryi* Shipp, 1896a, by monotypy.
= *Neopachysoma* Ferreira, 1953a. Type species: *Pachysoma denticolle* Péringuey, 1888, by original designation.
Last review: Entire genus reviewed by Harrison et al. (2003) as *Scarabaeus* (*Pachysoma*) with the inclusion of distributional and ecological data.

The long-established, flightless genus *Pachysoma* Macleay, 1821, differs strongly in appearance to winged members of the tribe Scarabaeini. However, it was recently reclassified as a subgenus of *Scarabaeus* Linnaeus, 1758, on the basis that the two genera cannot be differentiated morphologically after excluding characters associated with flightlessness, which include constriction between the reduced thorax and the anteriorly rounded abdomen that results from the loss of the humeral angles on the elytra. Subsequent combined morphological and molecular phylogenetic analysis resulted in the revalidation of *Pachysoma* as a full genus (Forgie et al. 2006).

Pachysoma is considered to be the most derived of the genera and subgenera in the tribe Scarabaeini. It currently comprises 13 valid species described between 1789 and 2003. Both molecular and morphological phylogenetic analyses support division of the genus into three species groups associated with particular soil type and climatic factors.

The genus is endemic to the dry to arid area below the escarpment along the West Coast from Cape Town in South Africa to Walvis Bay in central Namibia. Species have diversified primarily along a north–south axis between deep coastal sands of South Africa and southern Namibia (eight species), dune fields of the central Namib Desert in Namibia (three species), and the pre-Namib gravel plains in Namibia (two species).

Pachysoma is considered to have a Pliocene origin (2.9 MY) (Sole et al. 2005) associated with increased upwelling of the cold Benguela current and reduced rainfall followed by subsequent Plio–Pleistocene speciation events in response to cyclic climatic changes. The three resulting species groups show northern, central or mostly southern bias in ranges, but exceptionly, distributions of two species of the southern group are disjunct in the north centre of the generic range. Speciation has probably been influenced by vicariance across river barriers, environmental tracking during climatic change, or morphological adaptation to different landscapes and soil types from gravel to sands, either compacted or loose dune sands.

Behavioural differences to winged species of Scarabaeini support the treatment of *Pachysoma* as a full genus. All species are flightless and show diurnal foraging activity walking on the soil surface. Loss of flight and lower metabolic rate were possibly driven by increasing aridity on the West Coast and reduced availability of food. Whilst collection of dung pellets and dry portions of other dung types apparently dominates in five species, three species are characterised by mixed collection of dung pellets and vegetation detritus, and four species by a strong bias to collection of vegetation detritus, which may be more generally available than dung (Harrison et al. 2003). Several species have been observed to grip forage between the hind legs and drag it forwards to pre-constructed tunnels, which may be more energy efficient than the ball-rolling behaviour shown by their closest relatives and/or better suited to collection of detritus. It is unclear how the forage is treated for feeding purposes, but the triturating mouthparts of adults are able to ingest larger particles than most dung beetles. *Pachysoma* shows unique nesting behaviour within the subfamily Scarabaeinae, since larvae are free living in a cup-shaped mass of particles within a chamber in the soil. With the loss of brood ball construction that typifies ball-rolling dung beetles, larvae lack the characteristic dorsal hump found in species that develop within a dung ball.

Owing to relative aridity across the generic range, land usage is primarily grazing in natural vegetation and conservation, particularly in Namibia where almost the entire range of *Pachysoma* is conserved within national parks. In South Africa, only small parts of the ranges occupied by *Pachysoma* species coincide with national parks, or other reserves, and several species are comparatively unprotected. In the arid north, there is extensive grazing by livestock with threats from diamond mining along the coastline. In the moister south, cultivation, invasive exotic shrubs and urban development constitute

the greatest threat, particularly to the southernmost species, *P. aesculapius* Macleay, 1821. This species and two others with very restricted ranges are considered to deserve IUCN threat categories from Vulnerable (VU) to Endangered (EN). Further protection of these and four other species found in South Africa is desirable considering the restricted ranges and low vagility shown by the genus.

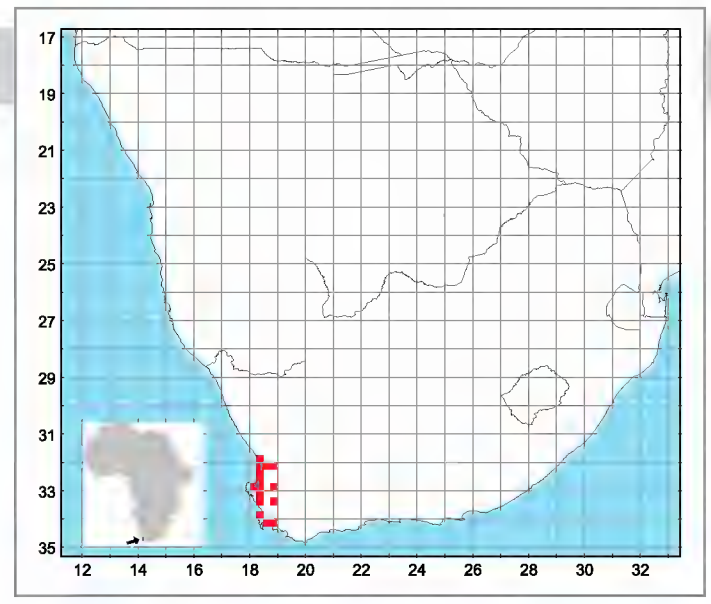
Pachysoma aesculapius

(Olivier, 1789)

= *Ateuchus barbatus* Thunberg, 1818
= *Pachysoma validum* Boheman, 1857

Global: VU (see IUCN Red List – VU)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: As *Scarabaeus aesculapius*: 'Cap' [Cape of Good Hope, South Africa], lectotype: 'no locality'; *A. barbatus*: Not stated; *P. validum*: 'Caffraria' [presumably South Africa].

Taxonomy: Accepted species; N–S cline in decreasing body size, but morphological variation does not support separation at species level; N individuals bear limited elytral indument.

Distribution: Restricted to a small area of coastal and inland sands in SW South Africa from the south bank of the Olifants River (N) to the Cape Flats, E of Cape Town (S).

Locality data (mean ± SD, range): Altitude: 134 ± 137, 0–502 m; annual rainfall: 259 ± 84, 178–466 mm; annual temperature (max. + min. /2): 17.0 ± 0.8, 15.8–18.4°C (N=26).

Habitat: No quantitative assessment; open shrubland on firm deep sands of coastal hummocks, river banks and vegetated dunes.

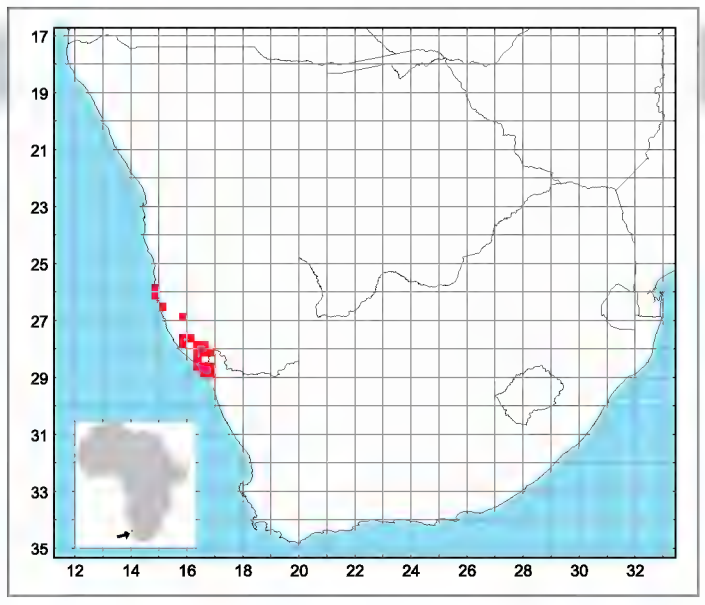
Food types: No quantitative assessment; seven excavated burrows contained only dry dung pellets.

Temporal activity: Flightless; diel activity diurnal; in SW Cape: seasonal activity in the moist spring (Aug. to Oct.) and dry summer (Nov. to Feb.); in mid-summer (Dec.): forages for short periods in the morning (07:00–09:00) and late afternoon (16:00–18:00) when radiant heat is lower than at midday.

Bioregions South Africa: Vegetation units of West Strandveld (FS 1, FS 5, FS 6), Sand Fynbos (FFd 2–5) (Fynbos Biome).

Assessment rationale: EOO = 10 750 km^2; AOO = ± 2 000 km^2; S part of range threatened by urban expansion around Cape Town (FS 6: 40%; FFd 5: 80% transformed) with no records from the City (Salt River), nearby Cape Flats and Somerset West since 1882–1886; much of the centre and N of range is threatened by conversion to arable lands and pasturage (FS 1, 5: 25–35%, FFd 2–4: 40–55% transformed); assessed as Vulnerable (VU).

Conservation measures: A quantitative survey to determine the exact AOO is advisable since distribution is probably localised on firmer deep sands and negatively influenced by loss of indigenous shrubland, through both agricultural and urban development, as well as invasive exotic vegetation; occurs in the provincial Rocherpan Nature Reserve and the coastal part of the Farm Modderrivier (60 km N of Cape Town), now run as the private Grotto Bay Nature Reserve; not found on looser coastal dune sands on the Farm Geelbek, now part of West Coast National Park; known occurrence within reserves is limited, so surveys should include the inland portion of West Coast National Park and the municipal protected coastal strip along False Bay.



Pachysoma bennigseni

Felsche, 1907

= *Pachysoma granulatum* Ferreira, 1953b

Global: LC
Endemic: RSA, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *P. bennigseni:* 'Oranjefluss' [presumably lower reaches of Orange River, SW Namibia]; *P. granulatum*: 'Daberas Dunes' [SW Namibia].

Taxonomy: Accepted species; Orange River is a geographical barrier between N and S populations although morphological differences are insufficient to justify separation at species level (N: larger, granular prothoracic disc; S: smaller, smooth prothoracic disc).

Distribution: Restricted to the arid N Succulent Karoo from the Holgat River mouth (NW coast, South Africa) to Spencer Bay, just N of Luderitz (Namibia); occurs no more than 60 km inland from the coastline in the S and central parts of its range; in the N, inland extent of the range narrows to the coastline along the S edge of the Namib Desert dune field.

Locality data (mean ± SD, range): Altitude: 287 ± 282, 11–991 m; annual rainfall: 41 ± 20, 2–75 mm; annual temperature (max. + min. /2): 15.5 ± 0.8, 14.0–16.9°C (N=24).

Habitat: No quantitative assessment; sparsely vegetated coastal sand dunes and sand flats that vary in nature from unstable to compacted sand.

Food types: No quantitative assessment; a single nest contained both dung pellets and detritus.

Temporal activity: Flightless; diel activity diurnal; recorded sporadically across all seasons.

Ecoregions Namibia: Centred on Succulent Karoo (AT1322).

Bioregions South Africa: Centred on two vegetation units: Richtersveld Coastal Duneveld (SKs 1), Richtersveld Red Duneveld (SKs 5) (Namaqualand Sandveld (SKs), Succulent Karoo Biome).

Assessment rationale: EOO = 8 500 km^2; known from 24 sites across a restricted but largely undisturbed and mostly protected range; therefore, assessed as Least Concern (LC).

Conservation measures: Assessement of conservation status would be improved by quantitative data on ecological associations; ± 90% of range protected by the Namib-Naukluft and Sperrgebiet national parks (Namibia) with the latter having restricted access since 1908; no protection in South Africa; coastal strip in S and centre of range heavily disturbed by open cast mining; unknown if there is any coastal bias in population density.

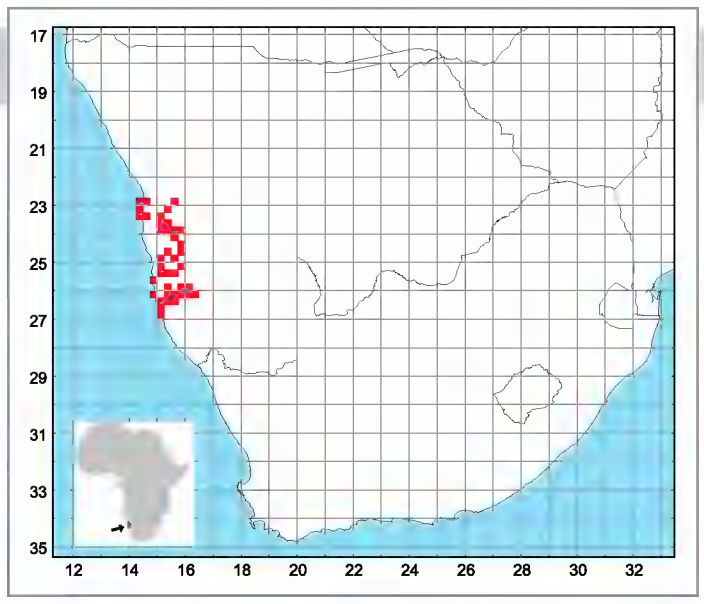
Pachysoma denticolle

Péringuey, 1888

= *Neopachysoma penrithae* Zunino, 1977

Global: LC (see IUCN Red List – LC)
Endemic: Namibia

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: *P. denticolle*: 'Walfish Bay' [Walvis Bay, central Namibia], lectotype: 'Walfish Bay, Namibia'; *N. penrithae*: 'Lüderitz' [SW Namibia].

Taxonomy: Accepted species; as variation in morphology shows no consistent geographical trend, the various populations are considered to represent a single species without subspeciation; variation comprises granular elytral interstriae in some S individuals and a N–S cline from red to melanic elytra.

Distribution: Restricted to the Namib Desert dune field, SW Namibia; dunes extend inland from the coastline to the gravel plains or base of the W escarpment from just N of Luderitz to just S of Walvis Bay.

Locality data (mean ± SD, range): Altitude: 589 ± 352, 0–1 145 m; annual rainfall: 47 ± 31, 0–89 mm; annual temperature (max. + min. /2): 16.1 ± 0.6, 14.9–17.2°C (N=58).

Habitat: No quantitative assessment; forages amongst sparse vegetation at the bases of dunes in the cooler early morning, which is consistent with other observations made in dune streets and on semi-stable sand; not observed on sand dunes.

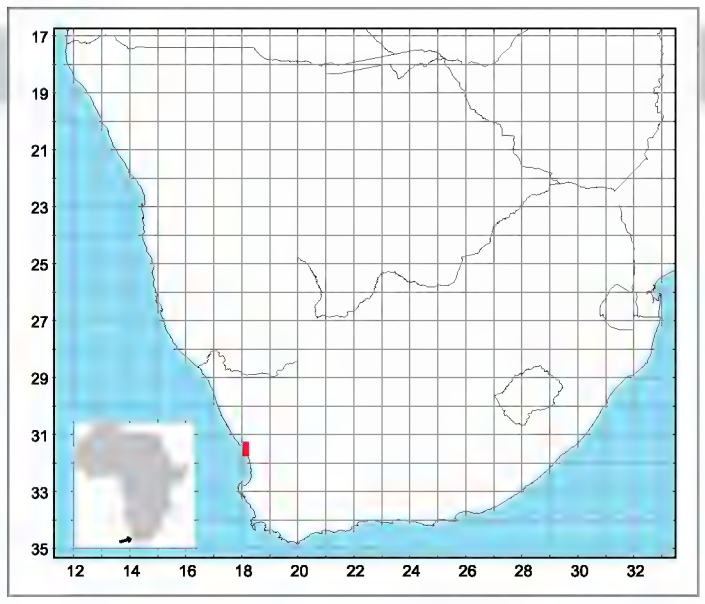
Food types: No quantitative assessment; forage picked up by hind legs and held under the abdomen whilst using front and middle legs for walking; collects mainly oryx and hare dung pellets, also droppings of chameleons, mice, dead insects and vegetable matter.

Temporal activity: Flightless; diel activity diurnal; no recorded seasonality in activity; collection records throughout the year.

Ecoregions Namibia: Centred on Namib Desert (AT1315).

Assessment rationale: EOO = 40 000 km^2; known from 68 sites across a somewhat restricted, but largely undisturbed, mostly protected range; no known threats, therefore, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; however, ± 95% of the range protected in the Namib-Naukluft National Park (Namibia).



Pachysoma endroedyi

(Harrison, Scholtz & Chown, 2003)

No synonyms

Global: EN (see IUCN Red List – EN)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Scarabaeus* (*Pachysoma*) *endroedyi*: 'Namaqualand, Kommandokraal Farm' [South Africa].

Taxonomy: Accepted species; smaller than the related *P. hippocrates* Macleay, 1821, from which it differs only by shorter metatarsal claws and elytral indument.

Distribution: Localised to an extremely small known range just north of the Olifants River, possibly, a little underestimated.

Locality data (mean ± SD, range): Altitude: 87 ± 34, 40–124 m; annual rainfall: 157 ± 2, 154–159 mm; annual temperature (max. + min. /2): 18.3 ± 0.1, 18.1–18.5°C (N=6).

Habitat: No quantitative assessment; open shrubland on the firm sand of coastal hillocks and dunes.

Food types: No quantitative assessment; of seven excavated nests, one contained dung pellets and six a mixture of pellets and vegetation detritus.

Temporal activity: Flightless; diel activity diurnal; recorded in the moist spring (Aug., Sept.) and dry summer (Dec., Jan.).

Bioregions South Africa: Margins of the Succulent Karoo (SK) and Fynbos (F) Biomes in only two vegetation units: Namaqualand Strandveld (SKs 7), Namaqualand Sand Fynbos (FFd 1).

Assessment rationale: EOO = 130 km^2; recorded from 12 sites across an extremely restricted known range with little official protection, although there are some small private reserves; the range is only 2% (FFd 1) to 10% (SKs 7) transformed, but is extensively grazed by livestock on farms; as no part of the small range is known to occur within a protected area, assessed as Endangered (EN).

Conservation measures: A quantitative survey is required to determine its ecological associations, AOO and population density within the restricted area of remaining suitable dune habitat to assess extinction risk; effects of recreational development around Strandfontein and Koekenaap require investigation. Not currently known from any protected area.

Pachysoma fitzsimonsi

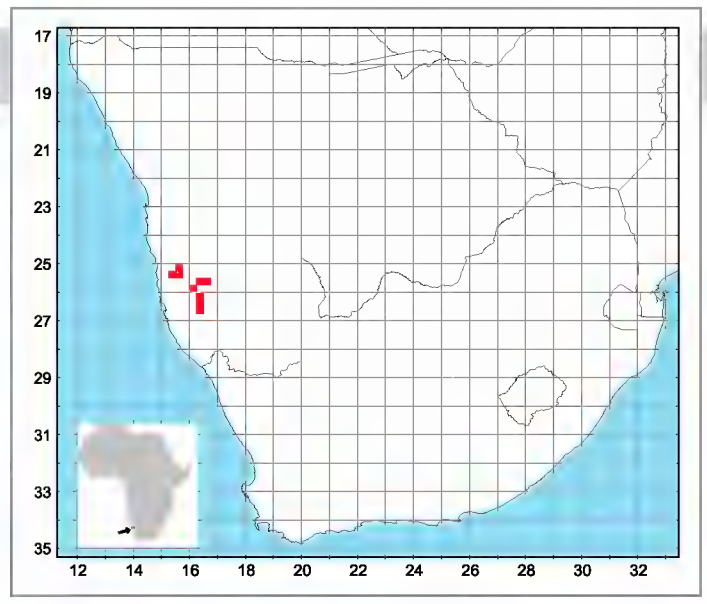
Ferreira, 1953a

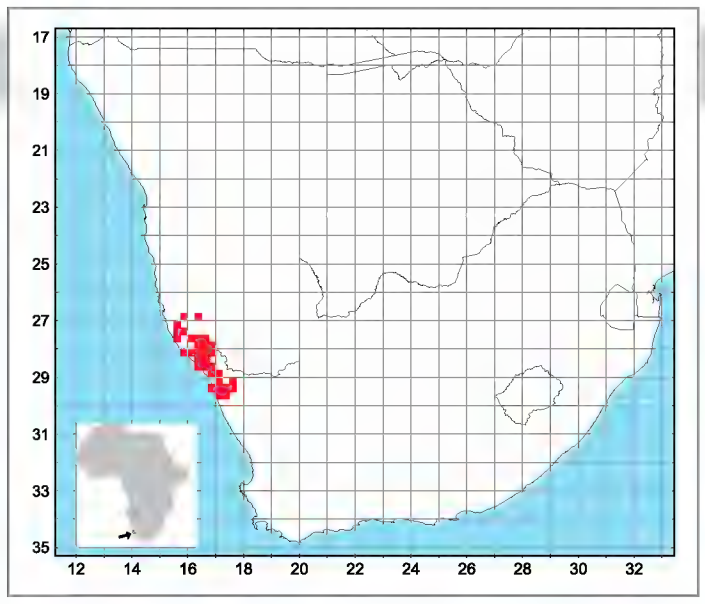
No synonyms

Global: LC (see IUCN Red List – LC)
Endemic: Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Namtib, 70 km NW of Aus' [farm in SW Namibia].
Taxonomy: Accepted species.
Distribution: Centred on pre-Namib gravel plains, which border the inland margin of the Namib Desert dune field at the base of the W escarpment, SW Namibia.
Locality data (mean ± SD, range): Altitude: 1 010 ± 255, 598–1 488 m; annual rainfall: 83 ± 26, 46–146 mm; annual temperature (max. + min. /2): 15.6 ± 0.4, 13.3–16.0°C (N=13).
Habitat: No quantitative assessment; arid, sparsely grassed, gravel plains or gravelly sands, with or without scattered shrubs.
Food types: No quantitative assessment; predicted to be dung pellets on the basis of morphological characters and supported by excavations of nests in a sparse-grass pasture grazed by sheep on the farm Weissenborn; also observations of tunnels clustered around concentrations of dung pellets that were being collected by *P. fitzsimonsi* in Namibrand Nature Reserve.
Temporal activity: Flightless; diurnal activity in the dry winter/spring (June to Oct.) and late summer (Feb., Mar.).
Ecoregions Namibia: Namib Desert (AT1315), marginal in Namibian Savanna Woodlands (AT1316).
Assessment rationale: EOO = 8 250 km^2; known from 16 sites across a somewhat restricted range, but would be supported by the dung of both wild herbivores and domestic livestock; assessed as Least Concern (LC) owing to the degree of protection in reserves.
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; however, ± 70% of the species range is protected within the Namib-Naukluft National Park and the private Namibrand Nature Reserve (Namibia); the remainder occurs on farms in the pre-Namib used for the grazing of livestock.





Pachysoma gariepinum

Ferreira, 1953a

No synonyms

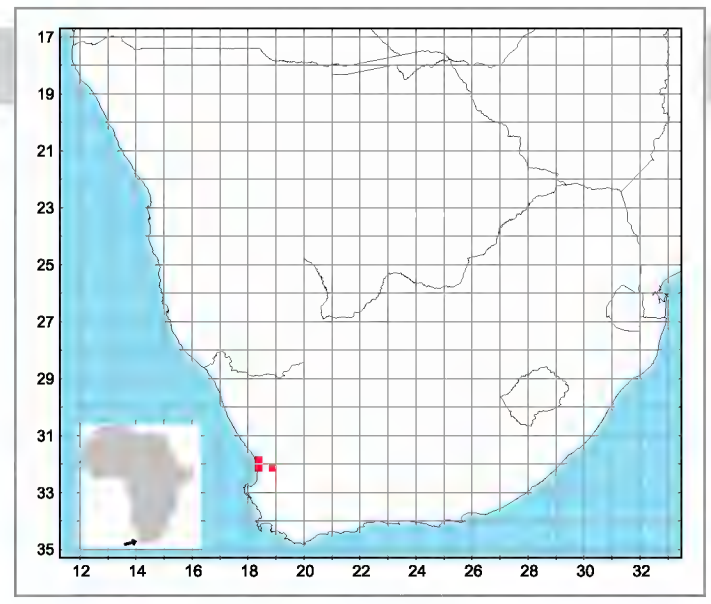
Global: LC (see IUCN Red List – LC)
Endemic: RSA, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Namaqualand: Holgat' [dry riverbed, NW South Africa].
Taxonomy: Accepted species; presence, relative prominence, or absence of a mesepisternal protuberance considered to represent a N–S cline in morphological variation within a single species.
Distribution: Distributed N and S of the Orange River [Gariep]; S range limits at the Buffels River (NW South Africa); northernmost locality at Agub Mountain (SW Namibia); present in coastal regions but 80% of records centred 20–35 km inland in South Africa; occurs up to 100 km inland in Namibia.
Locality data (mean ± SD, range): Altitude: 397 ± 273, 2.5–1 137 m; annual rainfall: 57 ± 17, 22–99 mm; annual temperature (max. + min. /2): 15.6 ± 0.8, 14.0–17.4°C (N=79).
Habitat: No quantitative assessment; centred on firm, consolidated deep sands of river banks, inland flats and at the base of rocky outcrops; found on dunes to the N of the Orange River, but not to the S.
Food types: Limited quantitative assessment; pre-constructs a tunnel then forages for food; of 17 excavated nests, nine contained dung pellets, three vegetation detritus and seven a mixture of the two; dry oryx (gemsbok) dung pellets are collected one at a time by dragging them forwards gripped between the hind legs; will also use dry horse dung from which it breaks a piece using the front legs and clypeus then drags it as for pellets.
Temporal activity: Flightless; diel activity diurnal; no recorded seasonality in activity; collection records throughout most of the year (Apr. to Jan.).
Ecoregions Namibia: Centred on Succulent Karoo (AT1322).
Bioregions South Africa: Centred on arid sands in the S Namib Desert (Desert Biome plus Succulent Karoo Biome: Richtersveld (SKr), N Namaqualand Sandveld (SKs)).
Assessment rationale: EOO = 17 650 km^2; known from 92 sites across a somewhat restricted range; South African range mostly coincides with farmland, but Namibian range largely undisturbed and protected; assessed as Least Concern (LC) owing to protection in Namibia.
Conservation measures: Assessment of conservation status would be improved by quantitative data on habitat associations; in Namibia: ± 90% of the range is protected within the Sperrgebiet National Park; the entire South African part of the range is unprotected with the most arid vegetation units considered in need of conservation due to sensitivity to degradation through grazing by livestock although possible effects on population density of *P. gariepinum* have not been tested.

Pachysoma glentoni

(Harrison, Scholtz & Chown, 2003)



No synonyms

Global: VU (see IUCN Red List – VU)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Scarabaeus* (*Pachysoma*) *glentoni*: 'Nortier Farm, SW Cape, South Africa'.

Taxonomy: Accepted species; very close to *P. hippocrates* Macleay, 1821, from which it is externally indistinguishable.

Distribution: Very restricted range extending along the coastal belt from just N of Lamberts Bay to just S of the Olifants River along whose banks the distribution extends inland almost to Clanwilliam.

Locality data (mean ± SD, range): Altitude: 136 ± 91, 39–342 m; annual rainfall: 191 ± 15, 171–214 mm; annual temperature (max. + min. /2): 17.9 ± 0.3, 17.5–18.3°C (N=9).

Habitat: No quantitative assessment; open shrubland on firm sand of river banks (Olifants, Groot Sandleegte) or coastal hummocks; not recorded in the vicinity of large dunes.

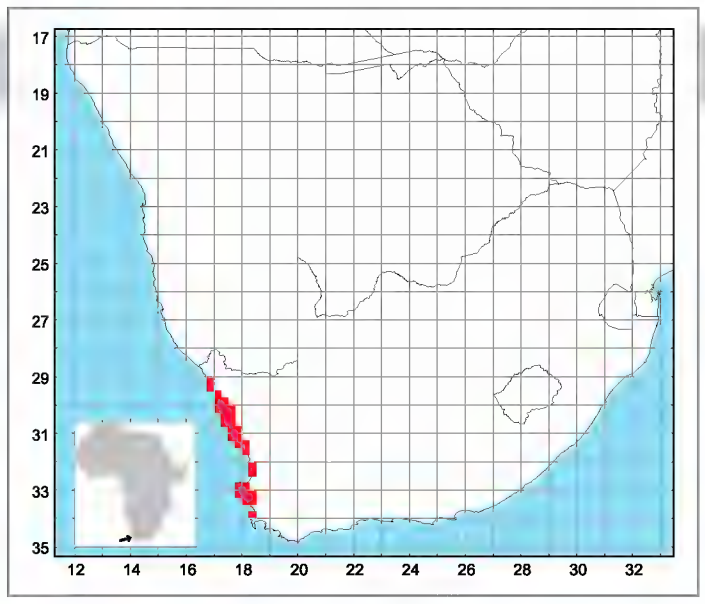
Food types: No quantitative assessment; grips detritus between hind legs and drags it to a pre-constructed burrow; one male observed in typical head-down, hind-legs-extended, pheromone-release stance, which may be used to attract females to the burrow entrance.

Temporal activity: Flightless; diurnal activity; recorded in the moist spring (July to Sept.) and dry summer (Nov., Dec.).

Bioregions South Africa: Occurs at the N edge of the Fynbos Biome in single vegetation units of Sand Fynbos (FFd) and Western Strandveld (FS): Leipoldtville Sand Fynbos (FFd 2), Lamberts Bay Strandveld (FS 1).

Assessment rationale: EOO = 700 km^2; known from only 12 sites that are centred on two vegetation units lacking official protection; however, there are some small private reserves; the range is 25% (FS 1) to 55% (FFd 2) transformed by cultivation and grazing by domestic livestock; assessed as Vulnerable (VU) owing to very small, largely unprotected, partly transformed range.

Conservation measures: A quantitative survey is required to determine the ecological associations and the AOO, which may reflect the amount of untransformed suitable habitat remaining within its range; the assessment should determine how much of the AOO coincides with private reserves, land grazed by livestock or land threatened by clearance for cultivation.



Pachysoma hippocrates

Macleay, 1821

= *Pachysoma macleayi* Castelnau, 1840
= *Pachysoma hessei* Ferreira, 1953a

Global: LC (see IUCN Red List – LC)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *P. hippocrates*: 'Cap Bonae Spei' [Cape of Good Hope, South Africa]; *P. macleayi*: 'Cap'; *P. hessei*: 'Wallekraal, Namaqualand' [farm in W South Africa].

Taxonomy: Accepted species; morphological and molecular variation along a N–S cline insufficient for division at species level either between four populations separated by major rivers or between S (typical *P. hippocrates*) and N populations (*P. hessei*) in which the inner protibial margin is elbowed and serrated S of the Olifants River with this character absent to the N.

Distribution: Restricted to arid W coastal strip, South Africa, from Bloubergstrand, N outskirts of Cape Town, to Port Nolloth in N Namaqualand; occupies a very narrow coastal strip in the N.

Locality data (mean ± SD, range): Altitude: 96 ± 77, 0–232 m; annual rainfall: 166 ± 78, 63–368 mm; annual temperature (max. + min. /2): 17.1 ± 1.1, 14.5–18.6°C (N=64).

Habitat: No quantitative assessment; soft to firm deep sand of vegetated coastal hummocks and hillocks, the periphery of dune systems, as well as river beds and banks. Found in open shrubland, but not in adjacent sparse-grass pasture cleared of shrubs (farm Geelbek, now part of West Coast National Park).

Food types: No quantitative assessment; of 36 excavated nests, contents comprised vegetation detritus (25), dung pellets (5) or a mixture of the two (6).

Temporal activity: Flightless, diel activity diurnal; seasonal activity in the moist spring (Aug. to Oct.) and dry summer (Nov. to Mar.).

Bioregions South Africa: Namaqualand Sandveld (SKs) (Succulent Karoo Biome), vegetation units of Western Strandveld (FS) and Sand Fynbos (FFd) (Fynbos Biome).

Assessment rationale: EOO = 8 500 km^2; only ± 10% of range protected; in the S: range threatened by urban development and agricultural interests (25–35% transformed); in the N, most unprotected areas little transformed (2–10%); currently assessed as Least Concern (LC) on basis of little transformation in the N.

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; in the S: recorded in the 1990s in West Coast National Park (gazetted 1998); also occurs in the Groen and Spoeg rivers area of Namaqua National Park (gazetted 2008); probably not seriously threatened over much of the range, but further protection desirable in both N and S, particularly as the EOO is under 20 000 km^2.

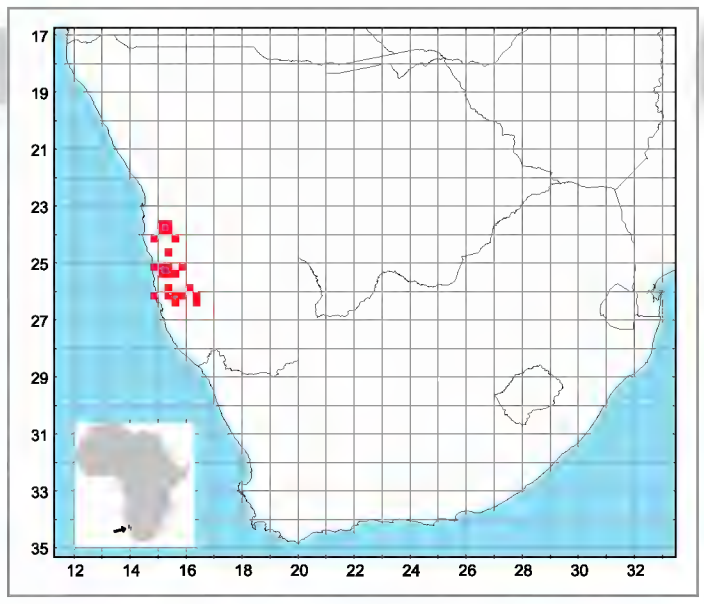
Pachysoma rodriguesi

(Ferreira, 1953a)

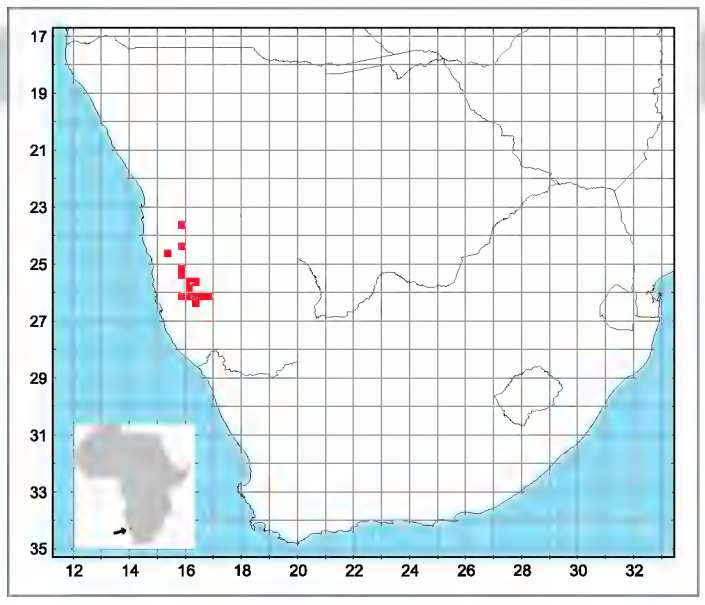
No synonyms

Global: LC
Endemic: Namibia

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: As *Neopachysoma rodriguesi*: 'Namtib' [farm, SW Namibia].
Taxonomy: Accepted species; some between-individual variation in the size of the protuberance on the frons.
Distribution: Restricted to Namib Desert dune field, SW Namibia; dunes extend inland from the coastline to the gravel plains or base of W escarpment from just N of Luderitz to just S of Walvis Bay.
Locality data (mean ± SD, range): Altitude: 555 ± 215, 2–1 145 m; annual rainfall: 40 ± 20, 0–89 mm; annual temperature (max. + min. /2): 16.2 ± 0.4, 15.6–17.0°C (N=44).
Habitat: No quantitative assessment; extreme psammophilous conditions on sparsely vegetated sand dunes as suggested by long legs with broadened or strongly setose tibiae for increased traction.
Food types: No quantitative assessment; collects dung pellets of hare and oryx (gemsbok).
Temporal activity: Flightless; diel activity diurnal; active in autumn, winter and spring (Mar. to Oct.), few records in the hot summer (only Jan.).
Ecoregions Namibia: Namib Desert (AT1315).
Assessment rationale: EOO = 24 000 km^2; known from 48 sites across a somewhat restricted, but largely undisturbed, mostly protected range; no known threats, therefore, assessed as Least Concern (LC).
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; however, ± 95% of the range protected in the Namib-Naukluft National Park (Namibia).



5 mm

Pachysoma rotundigena

Felsche, 1907

No synonyms

Global: LC
Endemic: Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Sinclair, SWA' [farm, SW Namibia].
Taxonomy: Accepted species.
Distribution: Restricted to the inland edge of the Namib Desert dune field, which extends inland from the coastline to the gravel plains or base of the W escarpment from just N of Luderitz to just S of Walvis Bay, SW Namibia.
Locality data (mean ± SD, range): Altitude: 1 021 ± 205, 665–1 319 m; annual rainfall: 89 ± 21, 45–124 mm; annual temperature (max. + min. /2): 16.1 ± 0.7, 14.9–17.5°C (N=18).
Habitat: No quantitative assessment; vegetated dunes at the inland margins of the dune field.
Food types: Unknown, but predicted to be a detritus feeder on the basis of morphology and habitat.
Temporal activity: Flightless; diel activity diurnal; no recorded seasonality in activity; active throughout most of the year.
Ecoregions Namibia: Namib Desert (AT1315), marginal in Namibian Savanna Woodlands (AT1316).
Assessment rationale: EOO = 9 500 km²; known from 19 sites across a restricted, but largely undisturbed range; no known threats, therefore, assessed as Least Concern (LC).
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; although ± 50% of the range is protected along the E margin of the Namib-Naukluft National Park and in the private Namibrand Nature Reserve (Namibia), a survey of its status on dunes in adjacent farmland would be useful.

Pachysoma schinzi

Fairmaire, 1888

No synonyms

Global: DD
Endemic: Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Namaqua-Land' [probably Great Namaqualand, southern Namibia, which is the origin of most known individuals]; the collector (Dr Hans Schinz) sampled 'd'Owambo, de Damara et de Namaqua'.

Taxonomy: Accepted species; marked sexual dimorphism in the morphology of the head; male has two large bifid clypeal projections that are reduced in the female to clypeal teeth, but prominence varies with body size.

Distribution: Restricted to upland plains of Huib-Hoch Plateau near Aus, SW Namibia, along W escarpment edge; full EOO uncertain.

Locality data (mean ± SD, range): Altitude: 1 397 ± 134, 1 176–1 533 m; annual rainfall: 89 ± 20, 71–131 mm; annual temperature (max. + min. /2): 14.0 ± 0.5, 13.3–14.9°C (N=9).

Habitat: No quantitative assessment; sparse grassland and open scrubland on gravel plains straddling the boundary between two ecoregions.

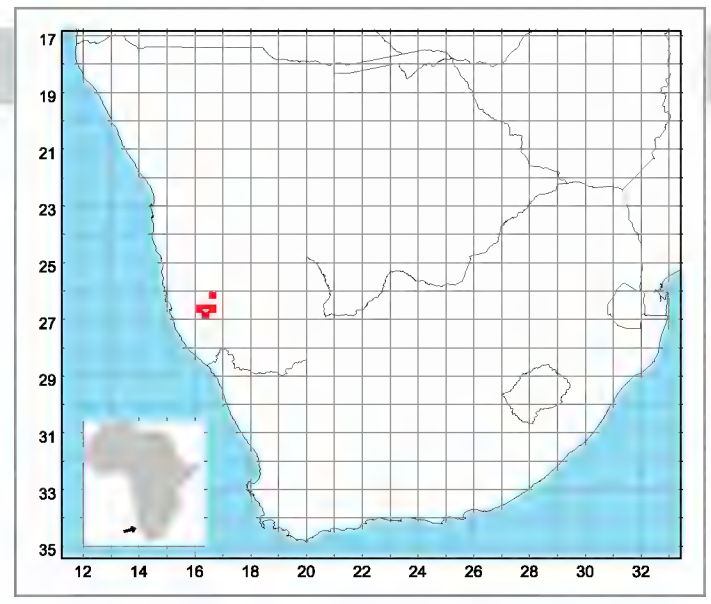
Food types: No quantitative assessment; recorded in farmland grazed by cattle, sheep and horses, but has been reported to feed on vegetation detritus.

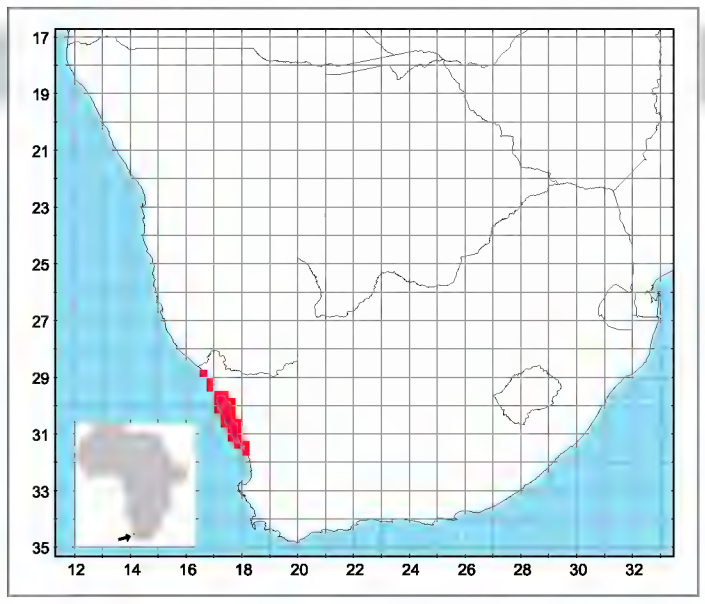
Temporal activity: Flightless; diel activity diurnal; active in spring (Sept. to Nov.) and late summer (Feb.); possibly a collecting artefact, possibly related to hot mid-summer temperatures.

Ecoregions Namibia: Margins of Nama Karoo (AT1314) and Namib Desert (AT1315).

Assessment rationale: EOO = 1 400 km^2; known from only 11 sites across a very restricted known range; most specimens recorded close to Aus; one further locality is interpreted as the nearby Tiras Plains having been wrongly cited as Tinkasflache; would probably qualify for an IUCN threat category of at least Vulnerable (VU) on the basis of small range in an unprotected region; however, currently assessed as Data Deficient (DD) owing to limited supporting information.

Conservation measures: Assessment of conservation status would be improved by a quantitative survey to determine the full EOO, AOO and ecological associations; currently known only from unprotected farmland used for the grazing of livestock where only 16% of the known reference material has been recorded since a large serial collection was made in 1950 (158 specimens; Harrison et al. 2003); low numbers may be an artefact related to low collecting effort or they may represent population decline in response to habitat modification resulting from farming operations.





Pachysoma striatum

Castelnau, 1840

= *Pachysoma marginatum* Péringuey, 1888
= *Irrorhotides fryi* Shipp, 1896a

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *P. striatum*: 'Cape' [Cape of Good Hope, South Africa]; *P. marginatum*: 'Port Nolloth, Namaqualand'; *I. fryi*: 'Port Nolloth' [both Port Nolloth, NW South Africa].

Taxonomy: Accepted species; differences in body size, elytral sculpture and relative development of elytral indument are considered to represent intraspecific morphological variation.

Distribution: Centred from three to 14 km from the coastline along W coastal zone, South Africa, between Holgat River in the N and Olifants River in the S.

Locality data (mean ± SD, range): Altitude: 113 ± 88, 0–609 m; annual rainfall: 114 ± 26, 52–159 mm; annual temperature (max. + min. /2): 17.3 ± 1.0, 14.5–18.5°C (N=85).

Habitat: No quantitative assessment; firm, consolidated deep sands on river banks, vegetated coastal hummocks, hillocks and dunes.

Food types: No quantitative assessment; forages for dung pellets (rodent, sheep) and portions of ostrich dung; of 28 excavated nests, 26 contained dry dung pellets and only two a mixture of pellets and vegetation detritus.

Temporal activity: Flightless; diel activity diurnal; seasonal activity recorded from autumn through winter and spring to early summer (May to Dec.).

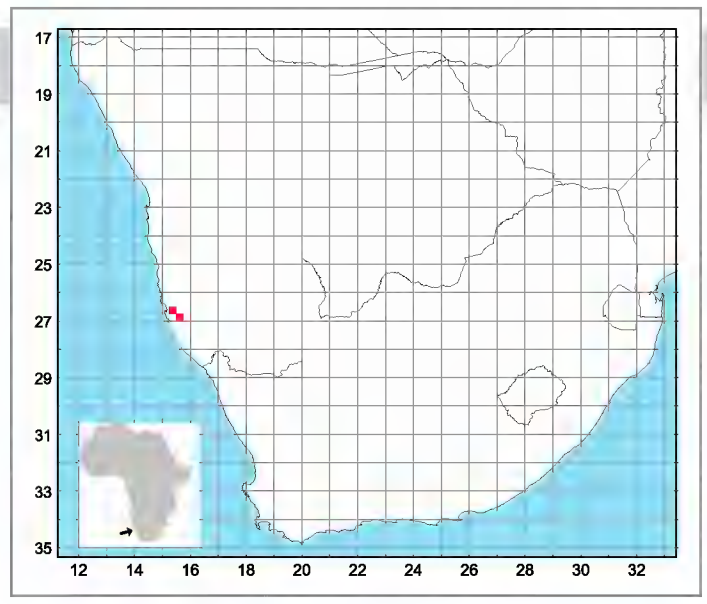
Bioregions South Africa: Centred on Namaqualand Sandveld (SKs) (Succulent Karoo Biome) with southern limits at the northern tip of Sand Fynbos (FFd) (Fynbos Biome).

Assessment rationale: EOO = 6 000 km^2; known from 150 sites across a somewhat restricted range of which a small part has received official protection since 2008; range subject to only 2–10% transformation, primarily through coastal mining, although there is extensive sheep grazing in SKs 7 and FFd 1; currently assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; ± 5% of the range is protected in the Groen and Spoeg river section of Namaqua National Park; of the remainder, the N range lies largely within the De Beers diamond concession and is subject to restricted access; the S range occurs on farms used primarily for the grazing of livestock; nevertheless, further protection would be desirable.

Pachysoma valeflorae

Ferreira, 1953a



No synonyms

Global: DD
Endemic: Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: '10m W of Haalenberg, Gt Namaqualand' [coastal mountain range in SW Namibia].

Taxonomy: Provisionally accepted species, but very close to *P. schinzi* Fairmaire, 1888; marked sexual dimorphism in the morphology of the head; male has two large clypeal projections that are reduced in the female to clypeal teeth.

Distribution: All but one of the specimens was recorded from around the coastal mountains of the Haalenberg and Rotkop, but the true extent of the range is uncertain; the suggestion of an E–W cline in morphological variation from Aus (*P. schinzi*) to the coast (*P. valeflorae*) is not currently supported since the species distributions are disjunct other than for one joint record from Tinkasflache, a clearly suspect and likely erroneous citation that has been interpreted as the Tiras Plains near Aus.

Locality data (mean ± SD, range): Altitude: 388 ± 98, 295–490 m; annual rainfall: 30 ± 4, 26–33 mm; annual temperature (max. + min. /2): 15.2 ± 0.1, 15.2–15.3°C (N=3).

Habitat: Unknown; possibly sand dunes.

Food types: Unknown.

Diel activity: Flightless; diel activity assumed diurnal like all other *Pachysoma* species; active in spring (Sept., Oct.), but seasonality, if any, unknown.

Ecoregions Namibia: Succulent Karoo (AT1322).

Assessment rationale: EOO = 200 km^2 (validated range); known by eight specimens from four sites (three validated) across an extremely restricted, but largely undisturbed known range; no known threats, but a poorly recorded species possibly because of low collecting intensity; assessed as Data Deficient (DD).

Conservation measures: A study is required to resolve questions on species status; assuming this is supported, a quantitative survey is required to assess conservation status; this should determine the full EOO, AOO and ecological associations; although known by very few specimens, no conservation actions are currently required as the entire known range is protected at the extreme N limits of the Succulent Karoo in the Spergebiet National Park.

Genus *Scarabaeolus* Balthasar, 1965a

Type species and designation: *Scarabaeus* (*Scarabaeolus*) *laevifrons* Fairmaire, 1884a, by original designation.
Synonyms: None.
Last review: Subgeneric status of *Scarabaeolus* (Balthasar 1965a) not recognised in a review (zur Strassen 1967) nor a checklist (Zídek & Pokorný 2004) of the genus, *Scarabaeus* Linnaeus, 1758; new species added to subgenus with synonymies (Deschodt et al. 2015b); raised to generic status (Moretto 2016b); new species and species list of *Scarabaeolus*, again, treated as a subgenus (Zídek & Pokorný 2018).

Scarabaeolus Balthasar, 1965a, was created as a subgenus of *Scarabaeus* Linnaeus, 1758, using a combination of characters. These include the absence of an overhanging elytral edge; two widely separated, parallel, lateral carinae on the elytra; small size (length: 10–14 mm); elytra tapering posteriorly, and the presence of two terminal mesotibial spurs (one vestigeal) as opposed to one. However, the subgenus was not recognised as a valid taxon in some subsequent taxonomic papers since both *Scarabaeus s. str.* and some *Scarabaeolus* possess a single mesotibial terminal spur, including the type species of *Scarabaeolus*. Nevertheless, following years of controversy, *Scarabaeolus* has now been raised to generic level on the basis of possessing an entire upper lateral elytral carena compared to an incomplete carena in other taxa (Moretto 2016b). Therefore, *Scarabaeolus* is treated here as a full genus.

When this book was completed at the end of 2017, *Scarabaeolus* comprised 33 valid species found in the Afrotropical region, although one NE African flightless taxon may be misplaced (*S. scholtzi* Mostert & Holm, 1982). Subsequently, further species were added by Zídek & Pokorný (2018) who, again, treated this taxon as a subgenus of *Scarabaeus* (see comments in Preamble). Most species show southern African centres of distribution although there are three exceptions. Two species are centred in NE Africa (Somalia), including the type species, *S. laevifrons*. A further newly described species, *S. davisianus* Moretto, 2016b, is centred in the Sahel (W and N central Africa). As a close, tropical, W African relative has an incomplete upper carena laterally on each elytron, it has recently (2016) been removed from *Scarabaeolus* and assigned to the revalidated genus *Parateuchus* Shipp, 1895e, as *P. palemo* (Olivier, 1789).

Both morphological and molecular phylogenies (Forgie et al. 2005, 2006) separate three *Scarabaeolus* species into a clade that is sister to those of other taxa in the tribe Scarabaeini. Behavioural differences to *Kheper* and *Scarabaeus s. str.* have been noted in pairs of *Scarabaeolus bohemani* (Harold, 1869b) where a female follows a ball rolled by the male as opposed to clinging to the ball rolled by the male. Available quantitative data suggest a bias to carrion (3), carrion + omnivore dung (3) or omnivore dung (3) with fewer found equally on omnivore and ruminant herbivore dung (2).

Of the 30 southern African species, 27 are found south of 15°S. Distribution patterns are primarily centred on deep sands although there are exceptions (*S. bohemani*, *S. megaparvulus* (Davis & Deschodt, 2015b)). Predominantly diurnal activity in hot, relatively dry systems may favour relatively smaller body size than in species of *Kheper* and *Scarabaeus s. str.* Furthermore, peak activity occurs especially after cooling rainfall events. Only two night-flying species are known (*S. canaliculatus* (Fairmaire, 1888); *S. flavicornis* (Boheman, 1860)).

Many species show distribution patterns centred on deep Kalahari sands (2) with bias to the arid SW (3), moister N (1), SE edge bordering the Highveld of South Africa (1) or additional occurrence in the pre-Namib (2) southwards to the SW coast (1). Other species have a distinct SW distributional bias in the SW Arid late summer rainfall region (1) with a bias to the S (4), or they are centred along the SW coast in the Western and Northern Cape (2), S Namib (2) or N Namib (2). A number of species show an E distributional bias in savanna bordering the Soutpansberg (2) or on the S Mozambique Coastal Plain (4). Exceptionally, *S. bohemani* shows an E, S and W circum-Kalahari distribution in the pre-Namib, Karoo and Savanna.

Threats to most of the 27 most southerly species are probably low as their distributions are centred on or partly extend into little-transformed or protected regions. Conservation status has been assessed as Least Concern (LC: 20 spp.) or Data Deficient (DD: 7 spp.).

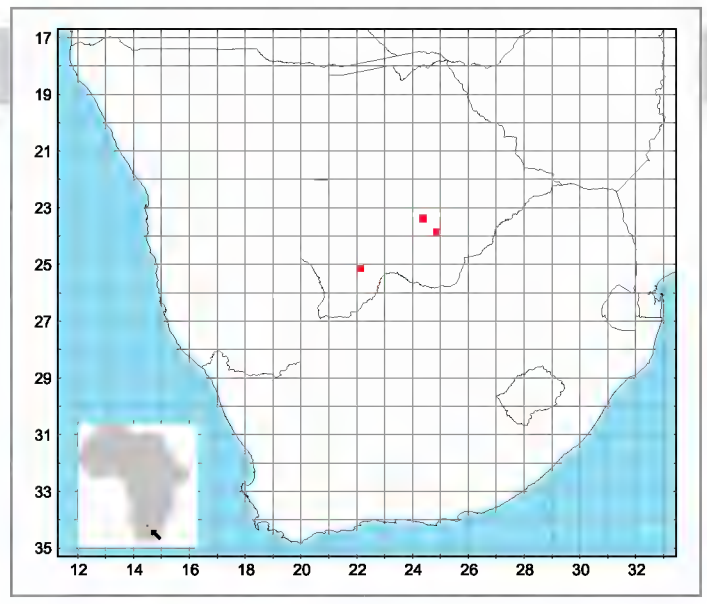
Scarabaeolus afronitidus

Davis, Stals & Deschodt, 2015

= *Scarabaeus* (*Scarabaeolus*) *nitidus* Davis & Deschodt, 2015b

Global: DD
Endemic: Botswana

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: *S. afronitidus*, *nom. nov.* for *S.* (*S.*) *nitidus* Davis & Deschodt, 2015b (pre-occupied name): 'Kutse Game Reserve' [Khutse Game Reserve, S central Botswana].

Taxonomy: Accepted species.

Distribution: Known from three localities in the SW Kalahari, SW Botswana.

Locality data (mean ± SD, range): Altitude: 1 004 ± 26, 987–1 035 m; annual rainfall: 347 ± 56, 283–386 mm; annual temperature (max. + min. /2): 20.5 ± 0.1, 20.4–20.6°C (N=3).

Habitat: No adequate quantitative assessment; in Botswana: sampled in low numbers (12) on deep sand in grassland with scattered shrubs.

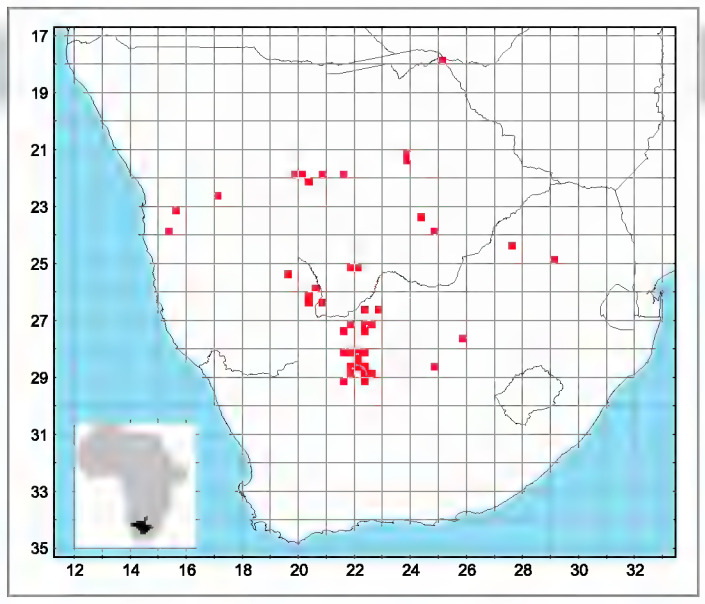
Food types: In Botswana: sampled primarily from omnivore dung: pig (10), rather than herbivore dung: elephant (1), sheep (1).

Temporal activity: Diel flight periodicity unknown, but presumably diurnal on the basis of black pilosity; recorded during the summer rainy season (Jan., Feb.).

Ecoregions Botswana: Kalahari Xeric Savanna (AT1309).

Assessment rationale: EOO = 9 250 km^2 (presumably underestimated); limited data suggest an arid, Kalahari sand specialist on omnivore dung, but further information is required to fully support the findings; therefore, assessed as Data Deficient (DD).

Conservation measures: Although all known records are from game reserves (Botswana: Khutse, Mabuasehube), this species remains poorly known; for a comprehensive assessment of conservation status, a quantitative survey of the SW Kalahari region is required to determine the full EOO and AOO, and to provide support for the currently limited data on ecological associations.



Scarabaeolus anderseni

(Waterhouse, 1890)

No synonyms

Global: LC
Endemic: RSA, Botswana, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Scarabaeus anderseni*: cited as 'Lake Nyassa' [Lake Malawi], but type labelled 'Lake Ngami'; the collector, 'Andersson' (not 'Andersen') sampled only from Damaraland, Ovamboland and Lake Ngami, and never went near Lake Nyassa.

Taxonomy: Accepted species; NW specimens show a green sheen becoming melanic to the SW.

Distribution: Known distribution centred on the SW Kalahari with additional records from the edge of the Namib Desert in Namibia, N Botswana, and deep sand outliers in Limpopo Province, South Africa; citations from Malawi and Zimbabwe require validation.

Locality data (mean ± SD, range): Altitude: 1 070 ± 164, 714–1 730 m; annual rainfall: 321 ± 138, 56–672 mm; annual temperature (max. + min. /2): 19.8 ± 1.3, 16.6–22.4°C (N=55).

Habitat: No adequate quantitative assessment; in Northern Cape: mostly restricted to SW Kalahari study sites (16) as opposed to Nama Karoo (1); recorded on deep sand (13) and sandy loam (4); essentially a deep sand specialist in open shrubland or grassland.

Food types: In Botswana: very strong bias to carrion (chicken livers: 322), attraction to dung much weaker (pig: 41, elephant: 5, cattle: 7, sheep: 15); one DBRU collection record of this species making a ball from the congealing blood of a dead snake supports carrion specialist habits.

Temporal activity: Diurnal flight activity during the late summer rainy season (Dec. to Mar.).

Ecoregions Namibia, Botswana: Centred on Kalahari Xeric Savanna (AT1309); also margins of three adjoining ecoregions.

Bioregions South Africa: Centred on Kalahari Duneveld (SVkd) and the deep sands that dominate the west of the Eastern Kalahari Bushveld (SVk) (Savanna Biome).

Assessment rationale: EOO = 627 900 km^2; AOO restricted to an extensive area of dry savanna on deep sands that is used primarily for the grazing of domestic livestock; in South Africa, there is little transformation in the two Kalahari Bioregions, particularly in the west; about 15% of the EOO coincides with reserves; currently assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by further quantitative data on habitat associations; protected within the boundaries of game reserves in Botswana and South Africa, including the Central Kalahari Game Reserve and Kgalagadi Transfrontier Park.

Scarabaeolus andreaei

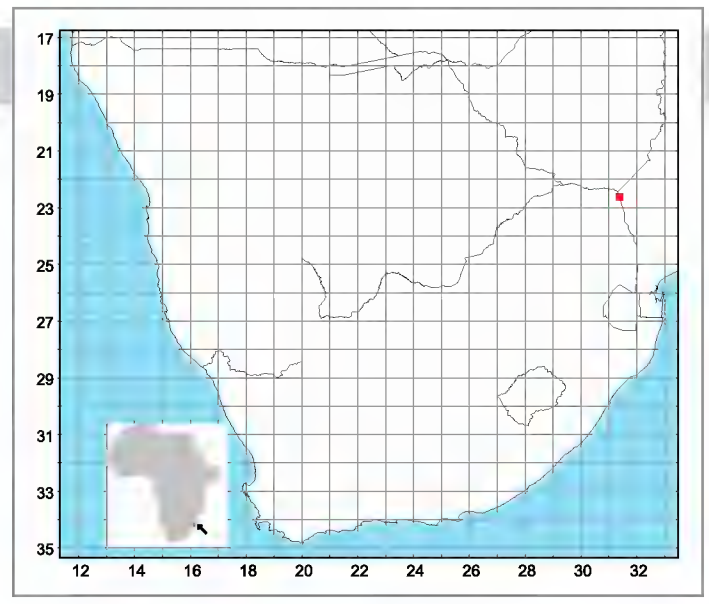
(zur Strassen, 1963)

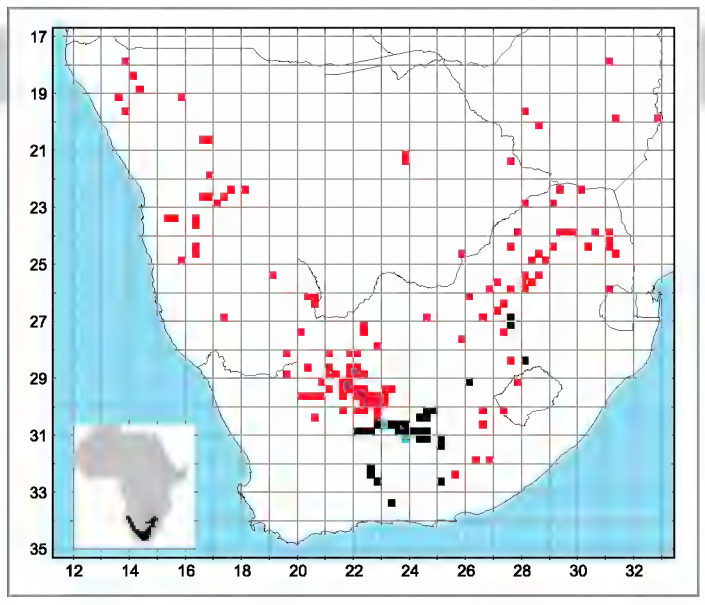
= *Scarabaeus xavieri* Ferreira, 1968

Global: LC (see IUCN Red List – DD for *Scarabaeus xavieri*)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Scarabaeus andreaei*: 'Inhambane, Mozambique'; *S. xavieri*: 'Província de Moçambique: Inharrime' [Mozambique].
Taxonomy: Accepted species with *S. xavieri* a recent synonymy.
Distribution: Known from coastal sands of S Mozambique and an inland sand outlier up the Limpopo River Valley (Nyandu Sandveld), which is the only known locality in South Africa.
Locality data (mean ± SD, range): Altitude: 83 ± 171, 0–429 m; annual rainfall: 835 ± 197, 479–1 084 mm; annual temperature (max. + min. /2): 23.6 ± 0.8, 22.9–25.2°C (N=6).
Habitat: No quantitative assessment; only recorded from deep sands; sampled in an open area within shrubland on coastal dune sand near Maçiene, Mozambique.
Food types: No quantitative assessment; sampled to pig dung.
Temporal activity: Diurnal flight activity during the summer rainy season (Dec., Jan.).
Ecoregions Mozambique: Southern Zanzibar-Inhambane Coastal Forest Mosaic (AT0128) (not shown on map).
Bioregions South Africa: Mopane (SVmp) (Savanna Biome).
Assessment rationale: EOO = 34 050 km^2; AOO probably limited by distribution of deep sands; protected in South Africa, but status in Mozambique uncertain; currently recorded as Least Concern (LC) on the IUCN Red List but essentially Data Deficient (DD).
Conservation measures: None required in South Africa where the extreme W edge of its range is protected in the N of the Kruger National Park; however, a survey is required to determine its full EOO, AOO and ecological associations on the Mozambique Coastal Plain, particularly the population sizes on deep sand patches compared to finer-grained soil types and the possible effects on conservation status of land usage along the coastline.





Scarabaeolus bohemani

(Harold, 1868b)

= *Ateuchus cicatricosus* Boheman, 1857

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: *S. bohemani*, *nom. nov.* for *A. cicatricosus*: 'Caffraria tota' [inexact, ?all of SE or southern Africa].

Taxonomy: Accepted species, but part of a species complex that includes the Sahel species, *S. davisanus* Moretto, 2016b, type locality 'St LOUIS Senég.' [Senegal, W Africa], and *S. obsoletepunctatus* Balthasar, 1940, type locality 'Benguela' [Angola]; original distribution cited for the related tropical W African species, *Parateuchus palemo* (Olivier, 1789), type locality, 'Senegal au Cap' [Senegal to the Cape of Good Hope], presumably includes data for *S. davisianus* and *S. bohemani*.

Distribution: South Africa, Lesotho, Namibia, Botswana, Zimbabwe; largely restricted to the summer rainfall region, but mostly absent from centre of the subcontinent occupied by deep Kalahari sands; elytral punctation variable from large pits with basal microgranulation, visible at × 10, through medium to fine pits with basal microgranulation invisible at macroscale; large pitted individuals in arid Upper Karoo and dry Highveld (black squares); medium pitted individuals widespread with cline to fine pitted individuals on arid W fringe of range (red squares); both varieties (blue square).

Locality data (mean ± SD, range): Red square: Altitude: 1 091 ± 273, 344–1 998 m; annual rainfall: 338 ± 204, 65–846 mm; annual temperature (max. + min. /2): 18.7 ± 1.6, 14.1–23.4°C (N=228). Black square: Altitude: 1 326 ± 175, 797–1 765 m; annual rainfall: 309 ± 109, 197–639 mm; annual temperature (max. + min. /2): 15.4 ± 1.0, 13.4–17.5°C (N=62).

Habitat: In Gauteng bushveld: primarily on sandy clay loam (79) as opposed to deep sand (1) and mainly in grassland (76) as opposed to open woodland (4) or shaded thickets (0); in Northern Cape: data suggest a soil generalist: sand (3.2), loamy sand (5.4), sandy loam (1.8), sandy clay loam (3.2); DBRU collection records also suggest a soil generalist and a bias to open vegetation: sand (10), sandy loam (9), sandy clay loam (5) in pasture/grassland (6), scrub/shrubland (12), open woodland (6).

Food types: No adequate quantitative assessment, but, in Botswana, biased to carrion (5) and pig dung (6) as opposed to herbivore dung: elephant (2), cattle (1), sheep (1); DBRU collection records on dung of human (2), baboon (1), horse (1), donkey (1), cattle (17), wildebeest (1).

Temporal activity: Diurnal flight activity; seasonal activity primarily during the summer rains (Oct. to Apr.); at Phalaborwa: activity greatest immediately in warm weather after heavy (24) or light rainfall (18), but lower under hot dry conditions (8).

Ecoregions Namibia, Botswana, Zimbabwe: Nama Karoo (AT1314), Namibian Savanna Woodlands (AT1316), SW Kalahari Xeric Savanna (AT1309), Kalahari Acacia-Baikiaea Woodlands (AT0709), Southern African Bushveld (AT0717), Zambezian Baikiaea Woodlands (AT0726), Southern Miombo Woodlands (AT0719), marginal occurrence in two other ecoregions.

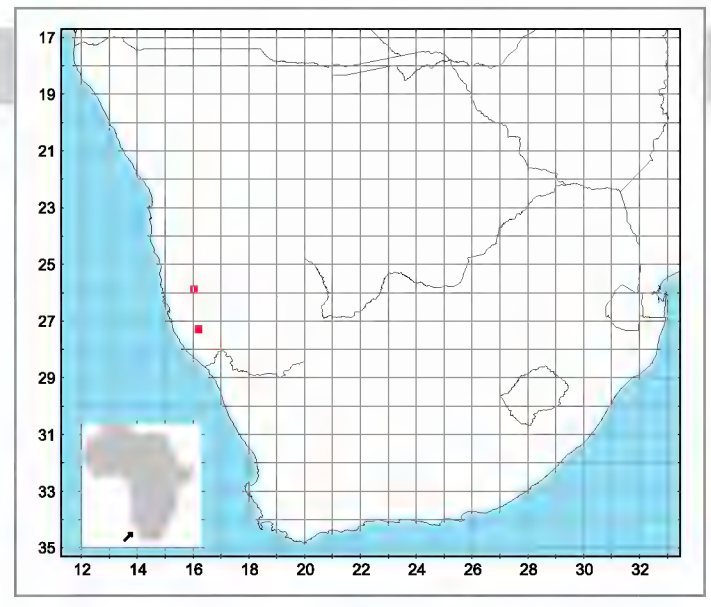
Bioregions South Africa: Red square: centred on Bushmanland (NKb), Kalahari Duneveld (SVkd), Eastern Kalahari Bushveld (SVk), Central Bushveld (SVcb), Mopane (SVmp); Black square: centred on Upper Nama Karoo (NKu), Lower Karoo (NKl); overlap zone in Dry Highveld Grassland (Gh); marginal in four other bioregions.

Assessment rationale: EOO = 1 063 280 km^2; widespread; mainly in more open vegetation at moderate altitude on various soil types; some vegetation units in NE part of South African range subject to transformation (Gh: 4–63%, SVcb: 2–49%, SVmp: 0–20%), but often very abundant after rainfall in the SW part of the range, which is little transformed (0–2% NKb, NKl, SVkd, W SVk), therefore, assessed as Least Concern (LC).

Conservation measures: None recommended as it is widespread and often abundant in both farmland and reserves; protected in various nature reserves, e.g. Roodeplaat, Abe Bailey, Leeuwfontein (South Africa); however possible taxonomic implications of the morphological variation should be investigated.

Scarabaeolus canaliculatus

(Fairmaire, 1888)



No synonyms

Global: LC
Endemic: Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Scarabaeus canaliculatus*: 'Namaqua' [interpreted as Great Namaqualand, southern Namibia, as it was described together with *Pachysoma schinzi* Fairmaire, 1888, a Great Namaqualand endemic].

Taxonomy: Accepted species; not to be confused with the recently revalidated *S. reichei* Waterhouse, 1890, from the SW Cape, South Africa (but see comments in Taxonomy section for *S. reichei*).

Distribution: Sporadically recorded in the southern Namib Desert, Namibia, which is consistent with a Great Namaqualand type locality.

Locality data (mean ± SD, range): Altitude: 894 ± 160, 782–1 007 m; annual rainfall: 67 ± 21, 52–81 mm; annual temperature (max. + min. /2): 15.3 ± 0.4, 15.0–15.6°C (N=2).

Habitat: No quantitative assessment; one record from dunes, another from the edge of a pan.

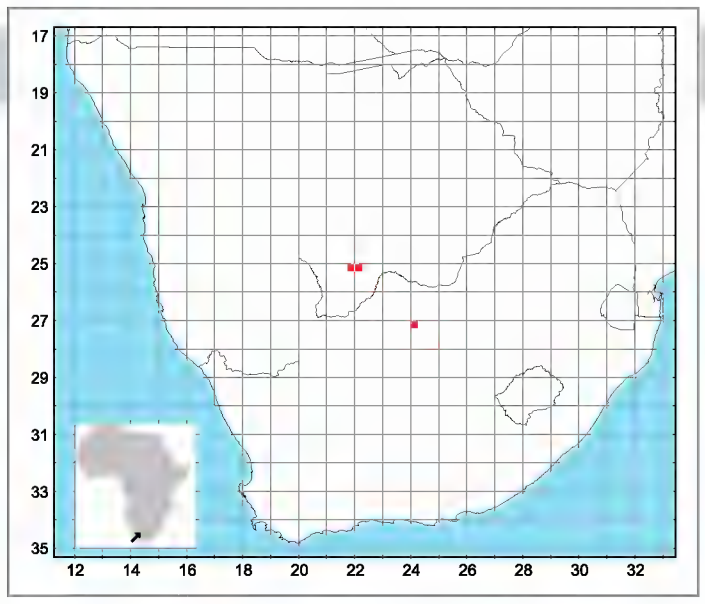
Food types: Not known.

Temporal activity: Diel flight periodicity unknown, but tan-coloured pilosity is indicative of flight activity during darkness; recorded during the late summer rainy season (Mar.).

Ecoregions Namibia: Range straddles the boundary between Namib Desert (AT1315) and Succulent Karoo (AT1322).

Assessment rationale: EOO = 910 km^2 (presumably underestimated); although this species may occupy a relatively small EOO and AOO below the W escarpment in SW Namibia, the two known exact records probably represent a collecting artefact rather than any particular rarity within this range; assessed as Least Concern (LC) rather than Data Deficient (DD) since the few known localities occur within a large reserve.

Conservation measures: Assessment of conservation status would be much improved by a survey to determine the full EOO and AOO including quantitative data on ecological associations; both known, exact records occur within the boundaries of the Namib-Naukluft or Sperrgebiet National Parks (Namibia).



Scarabaeolus carniphilus

(Davis & Deschodt, 2015b)

No synonyms

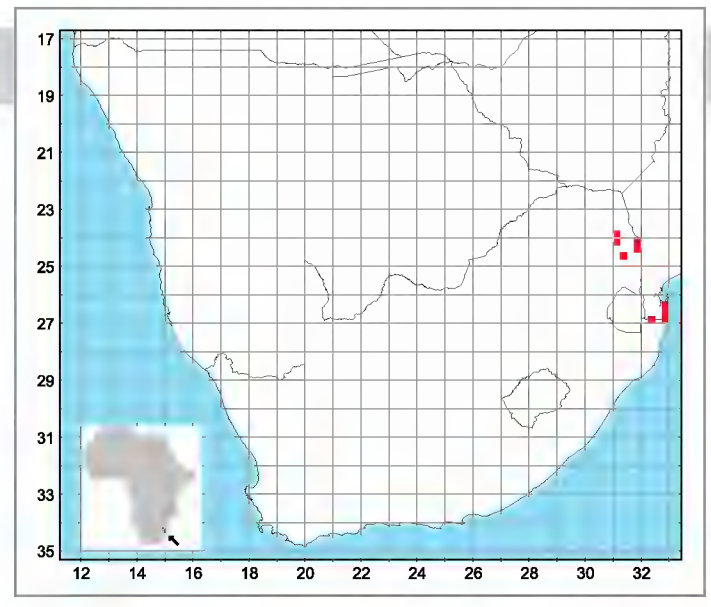
Global: DD
Endemic: RSA, Botswana

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Scarabaeus* (*Scarabaeolus*) *carniphilus*: 'Mabuasehube Game Reserve, SW Botswana'.
Taxonomy: Accepted species.
Distribution: Known only from three SW Kalahari localities in SW Botswana and the Northern Cape, South Africa; probably poorly collected due to dietary specialisation.
Locality data (mean ± SD, range): Altitude: 1 135 ± 226, 987–1 395 m; annual rainfall: 334 ± 86, 283–433 mm; annual temperature (max. + min. /2): 19.4 ± 1.5, 17.7–20.4°C (N=3).
Habitat: No quantitative assessment; all three known localities occur on deep sands in pasture or arid grassland.
Food types: In Botswana: sampled to carrion (7) and sheep dung (2); one DBRU collection record from cattle dung.
Temporal activity: Diel flight periodicity unknown, but probably diurnal based on black pilosity; all specimens recorded during the late summer rainy season (Feb.).
Ecoregions Botswana: Kalahari Xeric Savanna (AT1309).
Bioregions South Africa: Eastern Kalahari Bushveld (SVk) (Savanna Biome).
Assessment rationale: EOO = 4 285 km^2 (underestimated); likely a carrion specialist restricted to the deep sands and open vegetation of the SW Kalahari; however, known by only 10 specimens from three localities, so must be assessed as Data Deficient (DD).
Conservation measures: A survey of the SW Kalahari is required to assess the conservation status of this species; this should determine its full EOO, AOO and provide quantitative data on its ecological habits; protected in Mabuasehube Game Reserve (Kgalagadi Transfrontier Park), Botswana.

Scarabaeolus clanceyi

(Ferreira, 1954d)



No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Scarabaeus clanceyi*: 'Manguzi River, near Maputa, Zululand' [KwaZulu-Natal, South Africa].

Taxonomy: Accepted species.

Distribution: Localised in open vegetation on particularly sandy soils at the S tip of the Mozambique Coastal Plain: NE South Africa, S Mozambique.

Locality data (mean ± SD, range): Altitude: 167 ± 195, 0–443 m; annual rainfall: 673 ± 98, 529–780 mm; annual temperature (max. + min. /2): 22.3 ± 0.3, 21.5–22.6°C (N=14).

Habitat: No adequate quantitative assessment of soil association; at Phalaborwa: observed on sandy soils primarily in open grassy patches with scattered shrubs and trees (111), few in dense vegetation (5); on deep sand at Maputo Elephant Reserve: primarily recorded in grassland of saline pans (53), uncommon in small forest patches (4) and absent from large forest patches (0).

Food types: At Phalaborwa: very strong bias to omnivore dung (pig: 110), rare on cattle dung (6), absent from elephant dung (0).

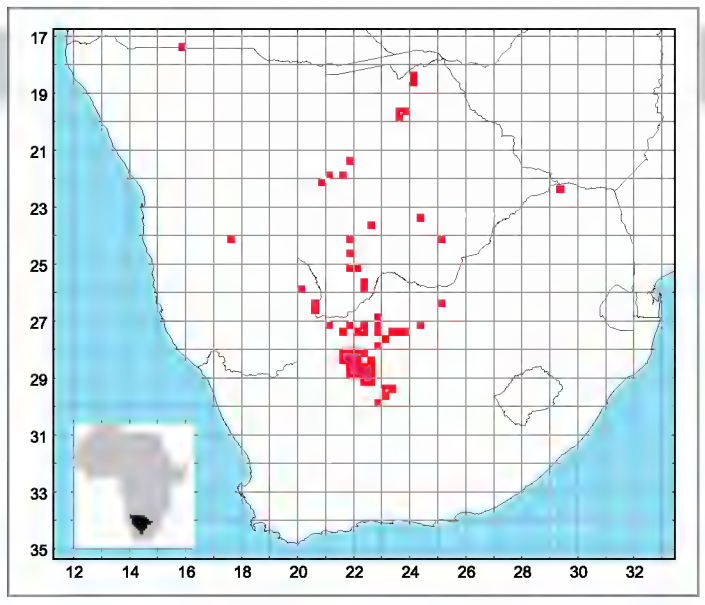
Temporal activity: Diurnal flight activity during the summer rainy season (Dec. to Feb.); at Phalaborwa: primarily active early on a dry sunny day two days after light rainfall (88), less active on a sunny day following very heavy rainfall (21), least on a cloudy day following light rainfall (7).

Ecoregions Mozambique: Localised in Maputaland Coastal Forest Mosaic (AT0119).

Bioregions South Africa: Localised in Mopane (SVmp), Lowveld (SVl) (Savanna Biome); Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 20 500 km^2; much of the known distribution occurs within conserved areas although it has also been recorded in relative abundance in communal grazing lands where the woodland has been opened up by collection of firewood; it would, therefore, face few current threats and is assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on soil associations, particularly to determine if the potential AOO is reduced by soil specialisation; however, most of the known AOO is protected in Maputo Special Reserve (Mozambique) and the central Kruger National Park (South Africa).



Scarabaeolus damarensis

(Janssens, 1940b)

= *Scarabaeus azureus* Ferreira, 1952a

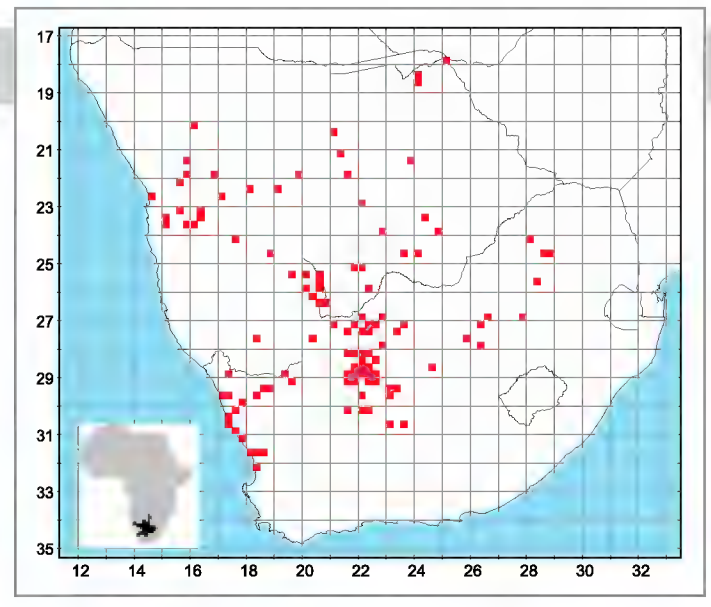
Global: LC (see IUCN Red List – LC as *Scarabaeus*)
Endemic: RSA, Botswana, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Scarabaeus damarensis*: 'Damara' [Damaraland, Namibia]; *S. azureus*: 'Ovampoland (Oshikango)' [Ovamboland, Namibia].
Taxonomy: Accepted species.
Distribution: Centred on the southern Kalahari, but several peripheral records suggest potentially wider occurrence that is possibly limited by specialisation to open vegetation on deep sands; much less abundant in wooded NE Botswana (27) than open vegetation of arid SW (1072); known distribution only South Africa, Botswana, Namibia.
Locality data (mean ± SD, range): Altitude: 1 078 ± 129, 596–1 402 m; annual rainfall: 297 ± 86, 174–599 mm; annual temperature (max. + min. /2): 19.7 ± 1.1, 17.9–22.7°C (N=113).
Habitat: No quantitative assessment; DBRU collection records primarily on deep sand (46), sandy loam (1) and primarily in open vegetation, pasture/grassland (16), scrub (12), shrubland (13), open woodland (6); northern outlier records mostly on floodplain grasslands.
Food types: In Botswana: primarily attracted to the dung of omnivores (pig: 341) and ruminant herbivores (cattle: 177, sheep: 297), less abundant on monogastric herbivore dung (elephant: 21) and carrion (chicken livers: 63); DBRU collection records on dung of human (1), cattle (23), wildebeest (1), sheep (1), horse (3), donkey (3).
Temporal activity: Diurnal flight activity during the summer rainy season (Oct. to Apr.).
Ecoregions Namibia, Botswana: Centred on Kalahari Xeric Savanna (AT1309), also open vegetation in Angolan Mopane Woodlands (AT0702), Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian and Mopane Woodlands (AT0725).
Bioregions South Africa: Centred on Kalahari Duneveld (SVkd), Eastern Kalahari Bushveld (SVk) (Savanna Biome).
Assessment rationale: EOO = 952 000 km^2; widely distributed in little-transformed (0–2%, SVkd, W SVk), dry areas of the SW Kalahari that are used primarily for conservation or the grazing of domestic livestock to which *S. damarensis* is readily attracted; therefore, assessed as Least Concern (LC).
Conservation measures: Assessment of conservation status would be improved by quantitative data on habitat associations, particularly to demonstrate how these influence the EOO and AOO; protected within the borders of Chobe National Park, Central Kalahari Game Reserve (Khutse), and Kgalagadi Transfrontier Park (Botswana and South Africa).

Scarabaeolus flavicornis

(Boheman, 1860)



No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Ateuchus flavicornis*: 'prope fluvium Svakop' [near Swakop River, W central Namibia].

Taxonomy: Accepted species.

Distribution: Centred on S Damaraland (Namibia), SW Kalahari, W coast and E marginal, Kalahari sand outliers (Botswana, South Africa); abundant on Liuwa floodplain grasslands (Zambia), but rare on lacustrine sands (Savuti, N Botswana), range probably dictated by specialisation to drier, open vegetation on deep sands; much less abundant in wooded NE Botswana (80) than open vegetation of arid SW (2 971).

Locality data (mean ± SD, range): Altitude: 988 ± 341, 0–1 782 m; annual rainfall: 272 ± 143, 9–799 mm; annual temperature (max. + min. /2): 19.1 ± 1.5, 15.2–22.4°C (N=178).

Habitat: In Gauteng: recorded exclusively on deep sand (11) not on sandy clay loam (0), primarily in grassland (10) as opposed to open woodland (1) or shaded thickets (0); supported by DBRU collection records: all records from deep sand (12) mainly in open vegetation: grassland (3), scrub (2), shrubland (4), open woodland (3).

Food types: In Botswana: extreme bias in attraction to carrion (chicken livers: 1 072) and pig dung (1 873) compared to herbivore dung, elephant (48), cattle (32), sheep (26); DBRU collection records from human (1), cattle (10) and donkey dung (1).

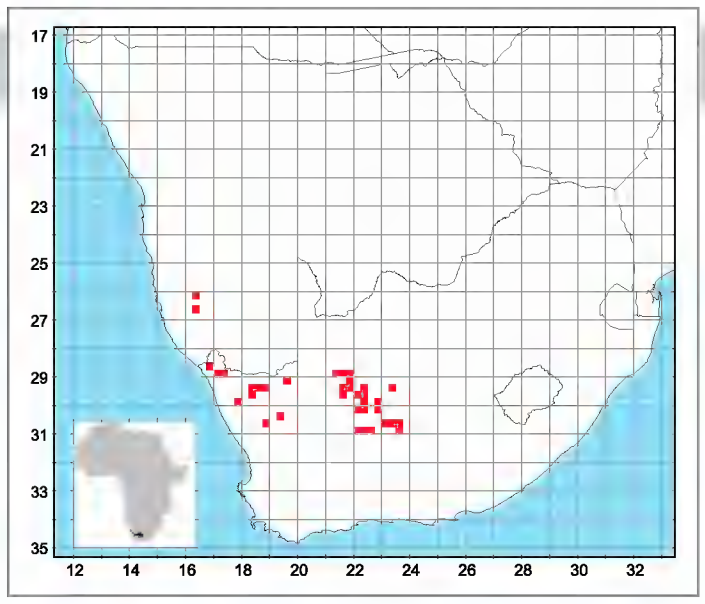
Temporal activity: Flight activity in darkness as indicated by the tan-coloured pilosity; recorded mainly during the summer rainy season in the NE (Oct. to May), also spring (Aug., Sept.) in the SW (winter rainfall region).

Ecoregions Namibia, Botswana: Centred on Kalahari Xeric Savanna (AT1309), central Namibian Savanna Woodlands (AT1316) with peripheral occurrence in four other ecoregions.

Bioregions South Africa: Centred on Kalahari Duneveld (SVkd), Eastern Kalahari Bushveld (SVk) (Savanna Biome); Namaqualand Sandveld (SVs) (Succulent Karoo Biome); N Upper Karoo (NKu), N Bushmanland (NKb) (Nama Karoo Biome); plus E sand outliers in Grassland and Savanna Biomes.

Assessment rationale: EOO = 844 500 km^2; wide distribution centred in little-transformed, arid areas used primarily for the grazing of domestic livestock to which it is attracted even though there is a much stronger bias to carrion and omnivore dung; assessed as Least Concern (LC).

Conservation measures: None required; about 5% of the range protected in the Central Kalahari Game Reserve (Botswana), Kgalagadi Transfrontier Park (Botswana, South Africa) and Namaqua National Park (South Africa).



Scarabaeolus fritschi

(Harold, 1868c)

No synonyms

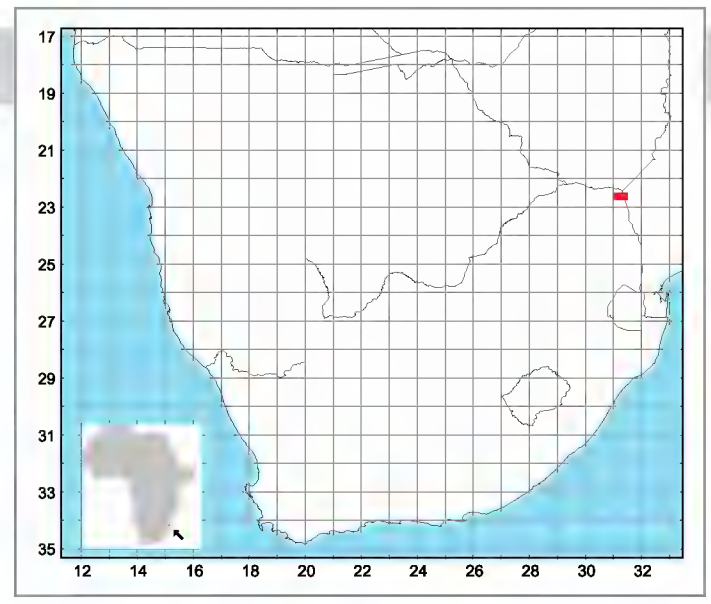
Global: LC
Endemic: RSA, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Scarabaeus fritschi*: 'Afric. Austral inter.' [interior of southern Africa].
Taxonomy: Accepted species.
Distribution: A wide E–W pattern of occurrence across the arid uplands in the centre of the Northern Cape, South Africa that swings northwards along the upper edge of the western escarpment into S Namibia; range mainly within the arid late summer rainfall region.
Locality data (mean ± SD, range): Altitude: 1 047 ± 228, 308–1 598 m; annual rainfall: 192 ± 55, 58–267 mm; annual temperature (max. + min. /2): 17.6 ± 1.4, 14.1–19.9°C (N=63).
Habitat: No quantitative assessment; observed on patches of arid deep or loamy sands, some piled against mountains, occurring as outlier dunes, fringing dunes of pans, or in beds of dry saline pans supporting grassland or a mixture of open scrub, shrubs and grassland.
Food types: No quantitative assessment; attracted to various dung types including those of cattle, sheep, horse.
Diel activity: Diurnal flight activity; spring (Aug. to Oct.) and autumn activity recorded (Feb., Mar.); absence of mid-summer records may be a collecting artefact.
Ecoregions Namibia: Nama Karoo (AT1314).
Bioregions South Africa: Centred on N Upper Karoo (NKu), Bushmanland (NKb) (Nama Karoo Biome); also Richtersveld (SKr), Namaqualand Hardeveld (SKn) (Succulent Karoo Biome) above W escarpment.
Assessment rationale: EOO = 110 000 km^2; AOO would be somewhat smaller owing to soil type specialisation; nevertheless the widespread occurrence of patches of sandy soils and attraction to the dung of domestic livestock on farms used primarily for grazing would mitigate for the small part of the range that occurs within protected areas; assessed as Least Concern (LC).
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; range little transformed (0–4% in South Africa); a small part is protected in the Richtersveld National Park and the Riemvasmaak Conservancy (South Africa).

Scarabaeolus gracai

(Ferreira, 1952a)



No synonyms

Global: DD

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Moçambique, Província do Sul do Save: Massinga' [Mozambique].

Taxonomy: Accepted species.

Distribution: Coastal sands of S Mozambique and sand outliers straddling the border of the Kruger National Park (South Africa) and Mozambique.

Locality data (mean ± SD, range): Altitude: 337 ± 158, 101–429 m; annual rainfall: 615 ± 267, 482–1 015 mm; annual temperature (max. + min. /2): 23.1 ± 0.2, 22.9–23.4°C (N=4).

Habitat: No quantitative assessment; recorded in unknown vegetation types on deep sand patches and coastal sands.

Food types: Not known.

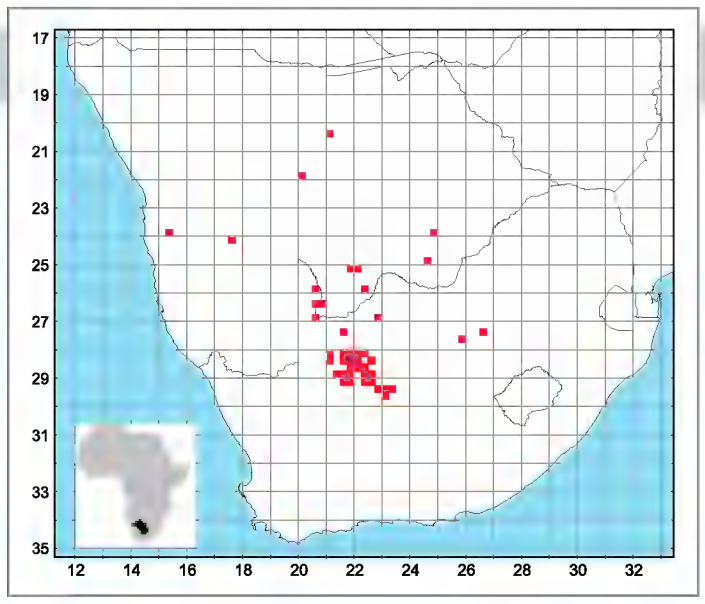
Temporal activity: Diel flight periodicity unknown, but assumed to be diurnal on the basis of black pilosity; recorded during the summer rainy season (Nov. to Apr.).

Ecoregions Mozambique: Sand localities: Southern Zanzibar-Inhambane Coastal Forest Mosaic (AT0128) (not shown on map).

Bioregions South Africa: Deep sand patches in Mopane (SVmp), N Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 3 040 km² (underestimated); known from only four localities; likely a deep sand endemic, but otherwise very poorly known; therefore, assessed as Data Deficient (DD).

Conservation measures: To assess its conservation status, a survey of the S Mozambique Coastal Plain is required; this should determine its full EOO, AOO and ecological associations; in South Africa, occurs only in entirely protected, deep sand outliers in the N Kruger National Park.



Scarabaeolus inoportunus

(Ferreira, 1953c)

No synonyms

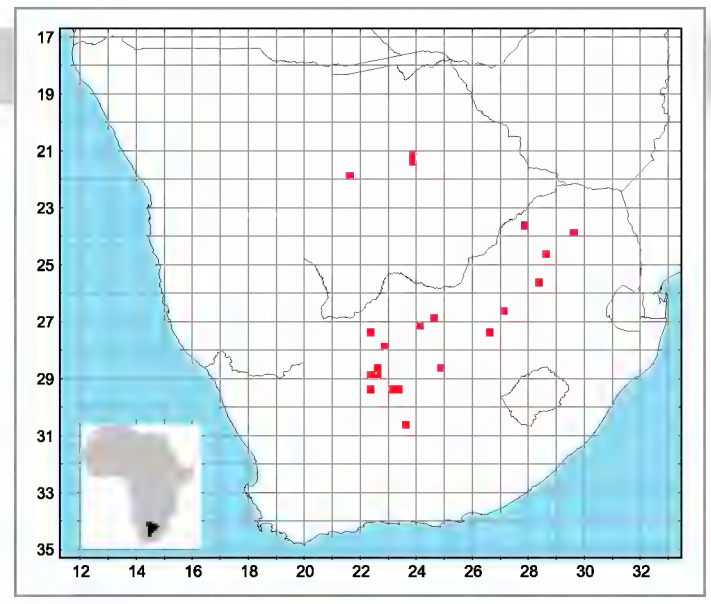
Global: LC (see IUCN Red List – LC as *Scarabaeus*)
Endemic: RSA, Botswana, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Scarabaeus inoportunus*: 'Província do Cabo: Griqualand West, Niekerk's Hope' [Niekerkshoop, Northern Cape, South Africa].
Taxonomy: Accepted species.
Distribution: Centred on the SW Kalahari with a bias to the arid SW; peripheral records in S Damaraland (Namibia) plus W Free State and North-West Province (South Africa).
Locality data (mean ± SD, range): Altitude: 1 055 ± 119, 714–1 349 m; annual rainfall: 257 ± 77, 56–555 mm; annual temperature (max. + min. /2): 19.4 ± 0.9, 16.6–22.0°C (N=67).
Habitat: No adequate quantitative assessment; observed in open shrubland and grassland on deep sands of plains, dunes and saline pans; at Brulpan: recorded primarily in grassland on an outlier Kalahari dune (966), rare in the surrounding Karoo shrubland on stony sand (1).
Food types: In Botswana: bias shown to omnivore dung (pig: 147) and ruminant herbivore pellets (sheep: 211) with carrion (chicken livers: 41), and dung of other herbivores (cattle: 64, elephant: 13) less attractive.
Temporal activity: Diurnal flight activity recorded in most months of the year (Dec. to Sept.); at Brulpan more abundant immediately after substantial rainfall (967) than under hot dry conditions (342).
Ecoregions Namibia, Botswana: Centred on the Kalahari Xeric Savanna (AT1309), also, SW margins of Kalahari Acacia-Baikiaea Woodlands (AT0709).
Bioregions South Africa: Centred on Kalahari Duneveld (SVkd), Eastern Kalahari Bushveld (SVk) (Savanna Biome); N Upper Karoo (NKu), N Bushmanland (NKb) (Nama Karoo Biome).
Assessment rationale: EOO = 510 500 km^2; wide distribution and ready attraction to the range of dung types available in the little-transformed, arid SW Kalahari (transformation 0–2% SVkd, W SVk) where grazing of domestic livestock and conservation dominate land usage; assessed as Least Concern (LC).
Conservation measures: Assessment of conservation status would be improved by further quantitative data on habitat associations; widespread on farms and protected within the Kgalagadi Transfrontier Park (South Africa, Botswana).

Scarabaeolus inquisitus

(Péringuey, 1908)

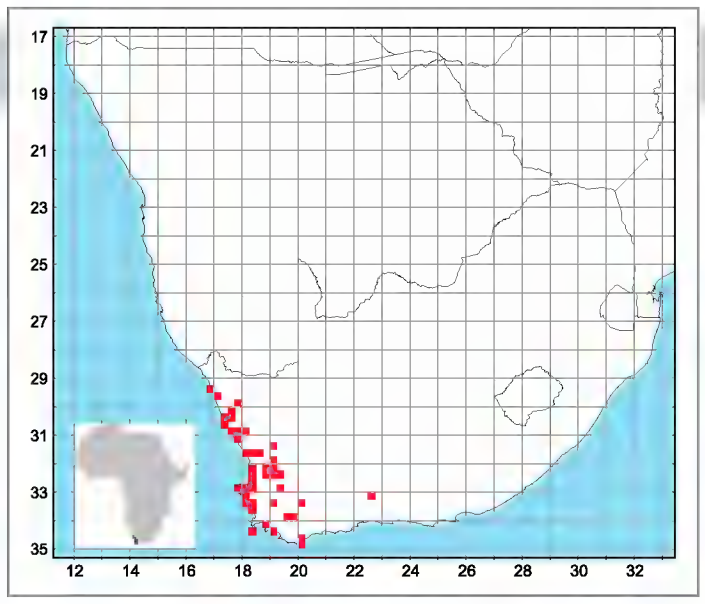


No synonyms

Global: LC
Endemic: RSA, Botswana

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'Transvaal (Potchefstroom, Plat River), Cape Colony (Vryburg)' [South Africa].
Taxonomy: Accepted species.
Distribution: Centred along the SE border of the S Kalahari (South Africa) with a few records from the Kalahari in central Botswana; unclear if the disjunct pattern is real or a collection artefact.
Locality data (mean ± SD, range): Altitude: 1 141 ± 154, 923–1 395 m; annual rainfall: 390 ± 134, 229–636 mm; annual temperature (max. + min. /2): 18.9 ± 1.6, 15.6–22.1°C (N=22).
Habitat: No adequate quantitative assessment; in Northern Cape: more abundant at four study sites on sand (27) than at four on sandy loam (4); all known records of vegetation type in grassland or shrubland (North Cape Survey, DBRU collection records).
Food types: No adequate quantitative assessment; in Botswana: recorded most abundantly to carrion (chicken livers: 9), and uncommonly to dung (pig: 1, elephant: 1, cattle: 2, sheep: 0).
Temporal activity: Diel flight periodicity unknown, but assumed to be diurnal on the basis of black pilosity; recorded primarily during the summer rainy season (Sept. to Mar., also May).
Ecoregions Botswana: Kalahari Acacia-Baikiaea Woodlands (AT0709).
Bioregions South Africa: Straddling parts of the Nama Karoo (NK), Grassland (G) and Savanna (SV) biomes: N Upper Nama Karoo (NKu); East Kalahari Bushveld (SVk), N Dry Highveld Grassland (Gh), Central Bushveld (SVcb).
Assessment rationale: EOO = 446 500 km^2; suspected to be a carrion specialist, primarily on deep sand patches in open vegetation, but range and ecological data inconclusive owing to limited records; apparent low population density may be an artefact of limited collection from carrion; assessed as Least Concern (LC) on basis of wide range but somewhat Data Deficient (DD).
Conservation measures: Assessment of conservation status would be improved by a survey to determine the full EOO and AOO as well as further quantitative data on ecological associations; protected in the N of the Central Kalahari Game Reserve (Botswana).



Scarabaeolus intricatus

(Fabricius, 1801)

No synonyms

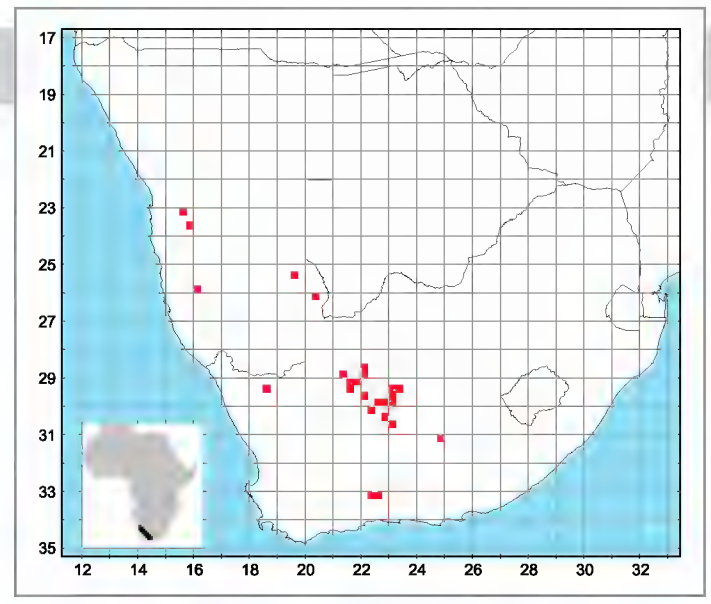
Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Scarabaeus intricatus*: 'Cap Bon. Spei' [Cape of Good Hope, South Africa].
Taxonomy: Accepted species.
Distribution: Centred on the coastal lowlands and western mountain escarpment in the winter rainfall region of South Africa, with one outlier record from the Eastern Cape that may indicate a wider continuous distribution in the bimodal rainfall region.
Locality data (mean ± SD, range): Altitude: 224 ± 269, 0–1 173 m; annual rainfall: 233 ± 100, 63–466 mm; annual temperature (max. + min. /2): 17.1 ± 1.1, 14.0–18.9°C (N=69).
Habitat: No adequate quantitative assessment; abundance in shrubland at Modderrivier (1 406) and Pampoenvlei (814) greater on deep sand than on sandy loam at Pampoenvlei (171); on arid deep sand at Geelbek: abundance in shrubland (247) strongly impacted by its clearance and replacement by sparse pasture grass (19); DBRU collection records: deep sand (5), sandy loam (2) in scrub (5) and pasture (2).
Food types: No quantitative assessment; DBRU collection records on dung of human (1), cattle (8).
Temporal activity: Diurnal flight recorded in all months (Aug. to May) except the coolest in mid-winter (June, July); in the SW Cape: sclerotised adults show a seasonal peak in early summer (Oct., Nov.), teneral adults in Jan. and Apr.
Bioregions South Africa: Centred on sandy soils of the Succulent Karoo (SK) and Fynbos (F) Biomes, especially: Namaqualand Sandveld (SKs), vegetation units of Western Strandveld (FS), Sand Fynbos (FFd), Sandstone Fynbos (FFs); also, margins of Rainshadow Valley Karoo (SKv).
Assessment rationale: EOO = 48 000 km^2 (W and SW localities); limited data and observations suggest a deep sand specialist in natural shrubland with a strong negative response to invasive exotic shrubs as well as the clearance of natural shrubland and its replacement by pasture grassland; probably threatened in S parts of its range, particularly in SW units of Sand Fynbos (FFd 2–7) and Western Strandveld (FS 1–6) where there is 25–80% transformation; currently assessed as Least Concern (LC) owing to little-transformed N of range.
Conservation measures: Assessment of conservation status would be improved by further quantitative data on ecological associations; protection is provided across ± 10% of its range in Cape of Good Hope Nature Reserve plus West Coast and Namaqua national parks (South Africa).

Scarabaeolus karrooensis

(zur Strassen, 1961b)

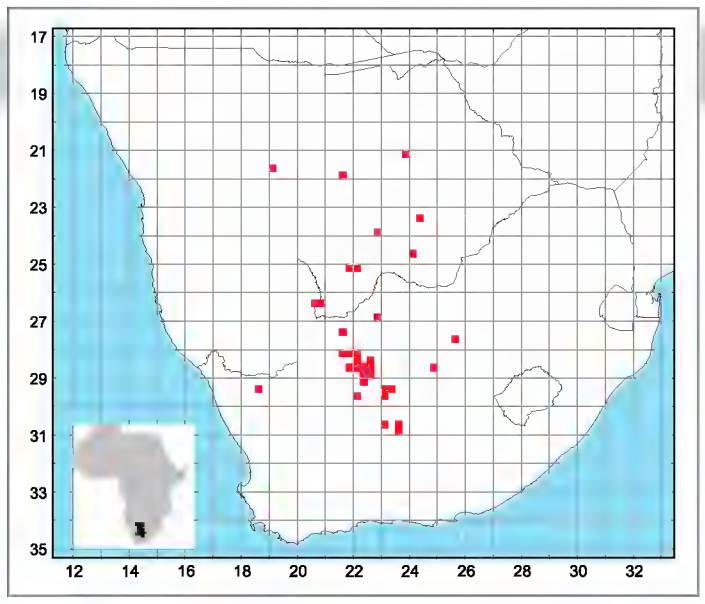


No synonyms

Global: LC (see IUCN Red List – LC as *Scarabaeus*)
Endemic: RSA, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Scarabaeus karrooensis*: 'Noupoort (=Naauwpoort) im Colesberg Distrikt' [Noupoort, Eastern Cape, South Africa].
Taxonomy: Accepted species.
Distribution: S of the arid late summer rainfall region and arid inland part of the bimodal rainfall region: SW South Africa, S Namibia.
Locality data (mean ± SD, range): Altitude: 1 019 ± 128, 617–1 527 m; annual rainfall: 210 ± 49, 81–348 mm; annual temperature (max. + min. /2): 18.5 ± 1.3, 13.9–21.3°C (N=45).
Habitat: No quantitative assessment; known from both sand dunes and finer-grained soils in scrub, but data too limited to determine if this species is a habitat generalist or specialist.
Food types: No quantitative data; a few records from mixed cattle/sheep dung baits.
Temporal activity: Diurnal flight activity during most months of the year (not mid-summer: Jan.; not mid-winter: July) reflecting a range across regions with either bimodal (spring/autumn) or late summer rainfall.
Ecoregions Namibia: SW Kalahari Xeric Savanna (AT1309), S Namibian Savanna Woodlands (AT1316).
Bioregions South Africa: Rainshadow Valley Karoo (SKv) (Succulent Karoo Biome); Upper Nama Karoo (NKu), N uplands Bushmanland (NKb) (Nama Karoo Biome); Kalahari Duneveld (SVkd) (Savanna Biome).
Assessment rationale: EOO = 359 300 km^2; widespread, but relatively poorly known, possibly because of confusion with close relatives; localities primarily from arid farmland used for grazing of domestic livestock; assessed as Least Concern (LC) because of the large range across a little-transformed region; however, essentially Data Deficient (DD).
Conservation measures: A survey across the full extent of Karoo regions is required to ascertain the full EOO and AOO. Assessment of conservation status would also be improved by quantitative data on ecological associations; protected in Kgalagadi Transfrontier Park (South Africa) and Namib-Naukluft Park (Namibia).



Scarabaeolus kochi

(Ferreira, 1952b)

No synonyms

Global: LC
Endemic: RSA, Botswana, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Scarabaeus kochi*: 'Kuke Pan' [waterhole in Botswana].
Taxonomy: Accepted species.
Distribution: Centred on the arid SW Kalahari in Botswana and the Northern Cape, South Africa, but possibly also with a continuous distribution further SW wherever deep sands occur.
Locality data (mean ± SD, range): Altitude: 1 094 ± 128, 876–1 485 m; annual rainfall: 274 ± 68, 100–479 mm; annual temperature (max. + min. /2): 19.1 ± 1.4, 15.1–22.1°C (N=53).
Habitat: No adequate quantitative assessment; in Northern Cape: higher frequency on deep, loamy or stony sands in grassland or open shrubland (n=1.0/trap at 37 sites) than on sandy loam (n=0.7/trap at 13 sites).
Food types: In Botswana: strongest bias to carrion (chicken livers: 148) and omnivore dung (pig: 74); less frequent on herbivore dung (elephant: 26, cattle: 28, sheep: 19); carrion bias supported by DBRU collection records on goat meat (1) and dead millipede (1).
Temporal activity: Diurnal flight activity in the late summer rainy season (Jan. to Mar.).
Ecoregions Namibia, Botswana: SE Kalahari Xeric Savanna (AT1309).
Bioregions South Africa: Centred on Kalahari Duneveld (SVkd), Eastern Kalahari Bushveld (SVk) (Savanna Biome); also deep sands bordering saline pans in N Upper Karoo (NKu) (Nama Karoo Biome).
Assessment rationale: EOO = 430 000 km^2; widespread in a little-transformed arid area that is either conserved or used for grazing domestic livestock; probably a sand specialist, but support from quantitative data required; assessed as Least Concern (LC) on the basis that deep sand habitat, carrion and various dung types would be widely available across its large EOO.
Conservation measures: Assessment of conservation status would be improved by further quantitative data on habitat associations; ± 15% of the known range protected in the Central Kalahari Game Reserve and Kgalagadi Transfrontier Park (Botswana and South Africa).

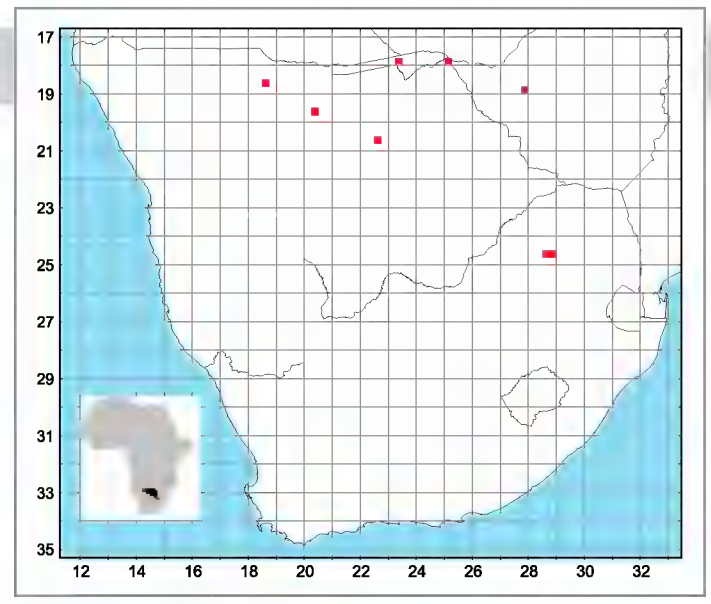
Scarabaeolus lucidulus

(Boheman, 1860)

= *Scarabaeus vansoni* Ferreira, 1958c

Global: DD

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: As *Ateuchus lucidulus*: 'juxta Lacum N'gami et fluvium Kuisip' [both near Lake Ngami, Botswana, and Kuiseb River, Namibia]; *S. vansoni*: 'Mangetti' [quarantine station, Ovamboland, Namibia].

Taxonomy: Accepted species; *S. vansoni* Ferreira, 1958c is a recent junior synonym.

Distribution: Scattered records in savanna on deep sands of Namibia, Botswana, Zimbabwe, South Africa.

Locality data (mean ± SD, range): Altitude: 1 020 ± 139, 707–1189 m; annual rainfall: 559 ± 75, 414–647 mm; annual temperature (max. + min. /2): 20.9 ± 1.5, 18.9–23.1°C (N=12).

Habitat: No quantitative assessment; all Namibia, Botswana and Zimbabwe localities map as deep sand; Nylsvlei localities recorded as sand; probably a deep sand specialist, possibly in open woodland.

Food types: No adequate quantitative assessment; at Nylsvlei: recorded to banana (16), carrion (7), human dung (4) and unspecified dung (1).

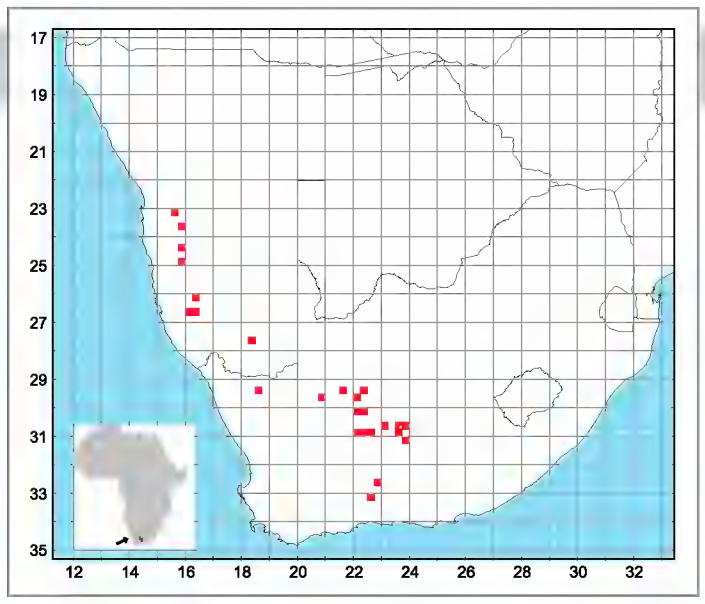
Temporal activity: Diurnal flight activity, primarily during the summer rainy season (Oct. to Mar.).

Ecoregions Namibia, Botswana, Zimbabwe: Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian Baikiaea Woodlands (AT0726).

Bioregions South Africa: Vegetation unit: Central Sandy Bushveld (SVcb 12) (Central Bushveld (SVcb), Savanna Biome).

Assessment rationale: EOO = 382 950 km^2 (dual type localities in Botswana and W Namibia suggest the EOO is underestimated); AOO presumed to be smaller according to occurrence of deep sand covered in woodland, which is, nevertheless, widespread across the range although SVcb 12 is 24% transformed; not well known, possibly owing to bias to rotting plant matter and animal carrion rather than dung; owing to limited information assessed as Data Deficient (DD).

Conservation measures: A quantitative survey is required to assess conservation status following the recent revision of the species taxonomy; the EOO, AOO and ecological associations have been hypothesised on the basis of limited observations; however, they are poorly known and require better support; protected in Nylsvlei Nature Reserve (South Africa).



Scarabaeolus megaparvulus

(Davis & Deschodt, 2015b)

No synonyms

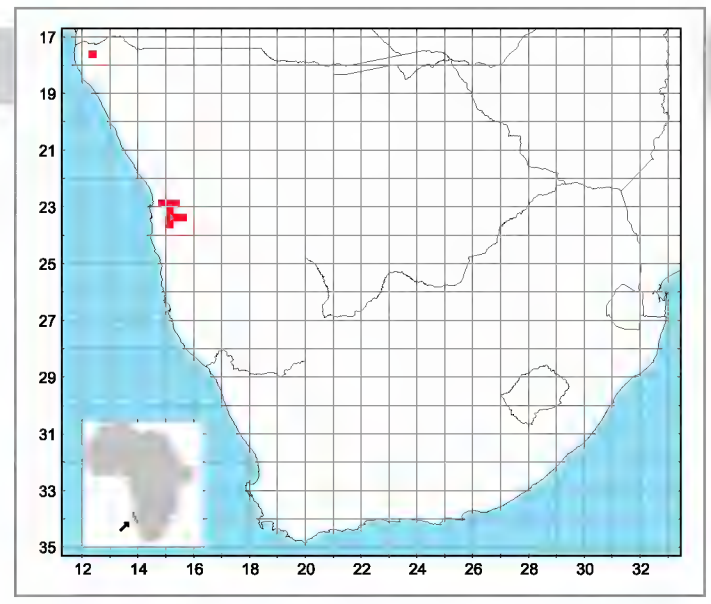
Global: LC
Endemic: RSA, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Scarabaeus* (*Scarabaeolus*) *megaparvulus*: 'Farm Rooiput' [Northern Cape, South Africa].
Taxonomy: Accepted species.
Distribution: Restricted to the arid late summer rainfall region; arid N foothills of the Swartberg, plateau of Upper Karoo in South Africa, and upper edge of the W escarpment in SW Namibia.
Locality data (mean ± SD, range): Altitude: 1 083 ± 241, 773–1 762 m; annual rainfall: 177 ± 65, 71–275 mm; annual temperature (max. + min. /2): 17.1 ± 1.8, 13.0–19.3°C (N=40).
Habitat: No adequate quantitative assessment; in Northern Cape: sampled from Upper Karoo and uplands S of Orange River, on both sand (1.3/trap, n=17 localities) and sandy loam or sandy clay loam (0.99/trap, n=14); DBRU collection records entirely from deep sand (6) in arid grassland (3), scrub (1), open woodland (1).
Food types: No quantitative assessment; sampled to mixed cattle/sheep dung baits; DBRU collection records from dung of cattle (1), donkey (1).
Temporal activity: Diurnal flight activity primarily during early/late summer in extreme S part of range (bimodal rainfall region) and late summer to the N in the arid late summer rainfall region (overall: Nov. to Mar.).
Ecoregions Namibia: SW margin of Namibian Savanna Woodlands (AT1316) overlooking the Namib Desert.
Bioregions South Africa: Higher-lying parts of N Bushmanland (NKb), Upper Karoo (NKu), Lower Karoo (NKl) (Nama Karoo Biome).
Assessment rationale: EOO = 59 650 km^2; a sizeable upland range across farmland in a little-transformed arid region used primarily for the grazing of domestic livestock to which this species is readily attracted; currently assessed as Least Concern (LC) owing to widespread records from cattle/sheep dung.
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; protected in hilly areas of the Namib-Naukluft National Park, Namibia; not so far recorded from any protected area in South Africa, but not currently considered to be threatened.

Scarabaeolus namibensis

(Zídek & Pokorný, 2018)

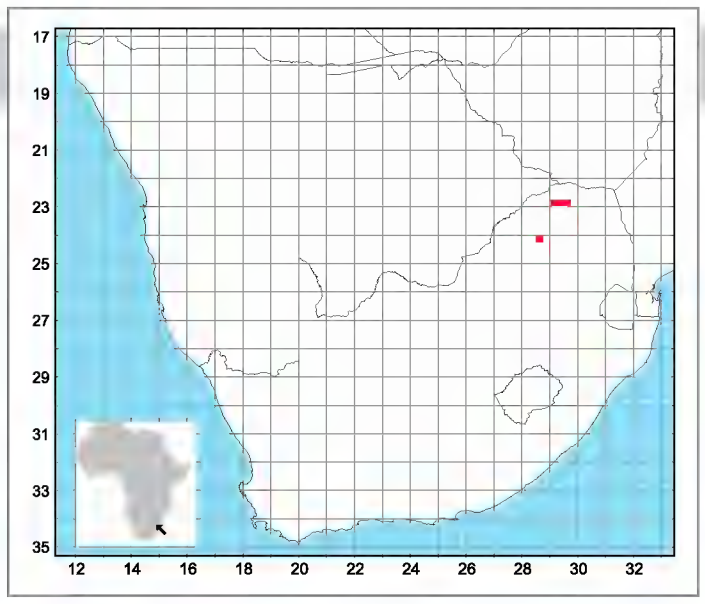


No synonyms

Global: LC
Endemic: ?Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Scarabaeus* (*Scarabaeolus*) *namibensis*: 'S.W. Afr. [Namibia], 60 km NE Gobabeb'.
Taxonomy: Accepted species.
Distribution: Currently known only from south of the Cunene River in two disjunct, arid, lowland population centres of the Kaokoveld in NW Namibia and the Namib Desert in W central Namibia.
Locality data (mean ± SD, range): Altitude: 577 ± 170, 309–910 m; annual rainfall: 60 ± 50, 27–228 mm; annual temperature (max. + min. /2): 16.7 ± 0.1, 16.5–16.9°C (N=15).
Habitat: No quantitative assessment; population in W central Namibia occurs on sparely grassed gravel plains of the Namib Desert.
Food types: No quantitative assessment; attracted to camel and pig dung.
Temporal activity: Diurnal flight activity; limited records in Sept., Jan. to Mar. and June insufficient to determine if activity is aseasonal like some other coastal desert *Scarabaeolus* species, e.g. *S. rubripennis* (Boheman, 1860).
Ecoregions Namibia: Kaokoveld Desert (AT1310), Namib Desert (AT1315).
Assessment rationale: EOO = 27 000 km^2; although known from only a few widely separated areas, this is probably a collection artefact; after light rain during an EIA study in June at Ongolo and Tumas (W central Namibia), there was a high local frequency of capture, which may suggest a continuous geographical distribution between population centres; assessed as Least Concern (LC) on basis of wide EOO.
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; also, a survey is required to determine if there is continuous N–S distribution including protected areas along the Skeleton Coast in the N Namib Desert; although the Kaokoveld locality lies outside of reserves, the central Namibian localities lie within the boundaries of the Namib-Naukluft National Park; whilst the southernmost of these localities remain protected, those to the north (Ongolo, Tumas) lie within an area scheduled for mining.



Scarabaeolus niemandi

(Deschodt & Davis, 2015b)

No synonyms (but see Taxonomy)

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Scarabaeus* (*Scarabaeolus*) *niemandi*: 'Soutpansberg, Limpopo, S22.87561° E29.73128°' [mountain range, Limpopo Province, South Africa].

Taxonomy: Accepted species; but see Preamble, notes with *Scarabaeolus rugosipennis* (Zídek & Pokorný, 2018).

Distribution: Only known from dry savanna on the N faces of the Blouberg, Soutpansberg and Waterberg, W Limpopo Province, South Africa; unclear if the distribution is continuous or disjunct.

Locality data (mean ± SD, range): Altitude: 1 006 ± 269, 804–1 478 m; annual rainfall: 521 ± 76, 460–651 mm; annual temperature (max. + min. /2): 19.6 ± 1.4, 17.1–20.6°C (N=5).

Habitat: No quantitative assessment; possibly a deep sand specialist in open woodland owing to records coinciding with sand at edge of Central Sandy Bushveld (SVcb 12) and Musina Mopane Bushveld (SVmp 2); also in Roodeberg Bushveld (SVcb 18) with mostly sandy soils.

Food types: No quantitative assessment.

Temporal activity: Diel flight periodicity unknown, but presumed to be diurnal on the basis of black pilosity; recorded during the summer rainy season (Nov., Feb.).

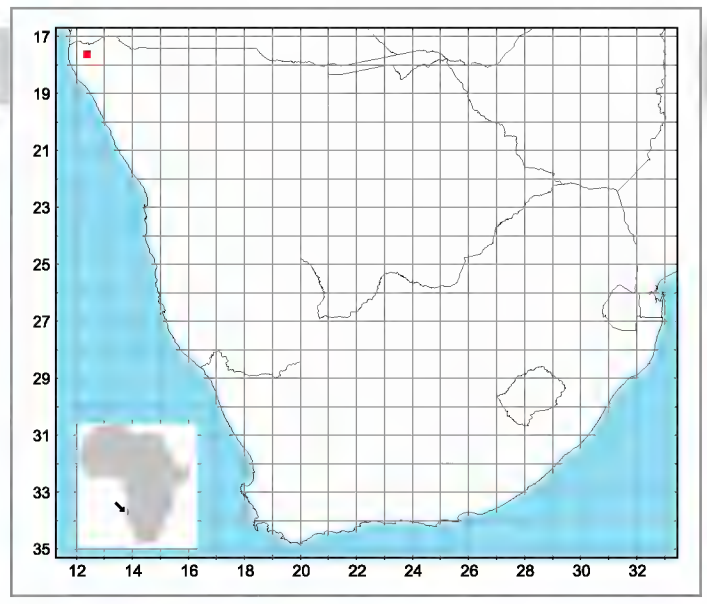
Bioregions South Africa: Mopane (SVmp), Central Bushveld (SVcb) (Savanna Biome).

Assessment rationale: EOO = 4 395 km^2 (underestimated); relatively poorly known species recently recorded from five localities with a known EOO < 5 000 km^2; AOO may be smaller according to occurrence of deep sand patches; transformation of range varies from 3% (SVmp 1), 18% (SVcb 18) to 24 % (SVcb 12), with the type locality scheduled for mining; although it would currently qualify for an IUCN threat category, it must be assessed as Data Deficient (DD) owing to the paucity of available information.

Conservation measures: To generate an assessment of conservation status, a quantitative survey of arid savanna in Limpopo Province is required to determine the full EOO; ecological associations also need to be determined from quantitative data as the AOO could be restricted to deep sand patches in open woodland; currently protected on the north slopes of the Blouberg Nature Reserve and the private Goro Nature Reserve.

Scarabaeolus obsoletepunctatus

(Balthasar, 1940)



No synonyms

Global: DD

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Scarabaeus obsoletepunctatus*: 'Angola, Benguella' [Benguela, Angola].

Taxonomy: Accepted species; a slightly larger-bodied, close relative of *S. bohemani* Harold, 1868, with largely effaced elytral punctation; individual pictured, here, requires validation as *S. obsoletepunctatus*.

Distribution: Arid coastal region of NW Namibia, SW Angola.

Locality data (averages): Altitude: 559 m; annual rainfall: 228 mm; annual temperature (max. + min. /2): 16.9°C (N=1).

Habitat: Not known.

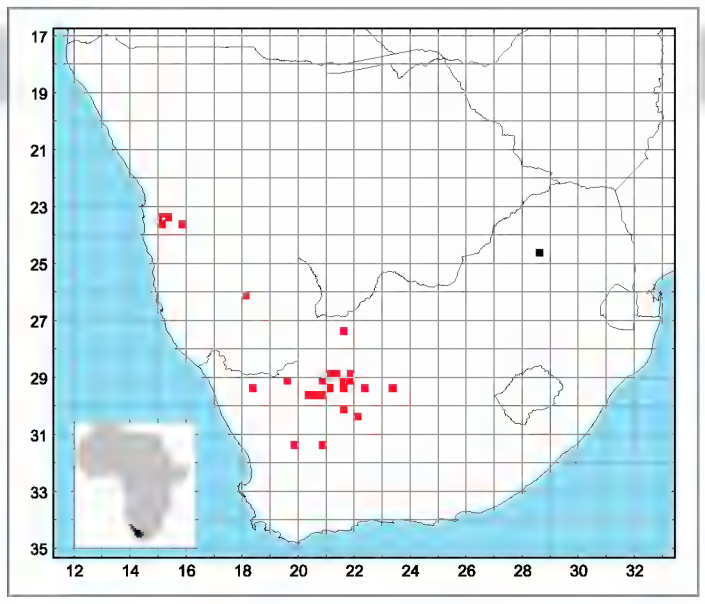
Food types: Not known.

Temporal activity: Diurnal flight activity presumed on the basis of black pilosity; recorded during the late summer rainy season (Feb.).

Ecoregions Namibia: One exact record from margin of Kaokoveld Desert (AT1310) and N Namibian Savanna Woodlands (AT1316).

Assessment rationale: EOO = 7 205 km² (underestimated, but EOO would be relatively restricted; probably mainly coastal SW Angola); very poorly known taxonomically, biogeographically and ecologically; assessed as Data Deficient (DD).

Conservation measures: To assess conservation status, a quantitative survey of the Kaokoveld and SW Angola is required; this needs to determine EOO, AOO and ecological associations; not currently known from any protected region.



Scarabaeolus pabulator

(Péringuey, 1908)

No synonyms

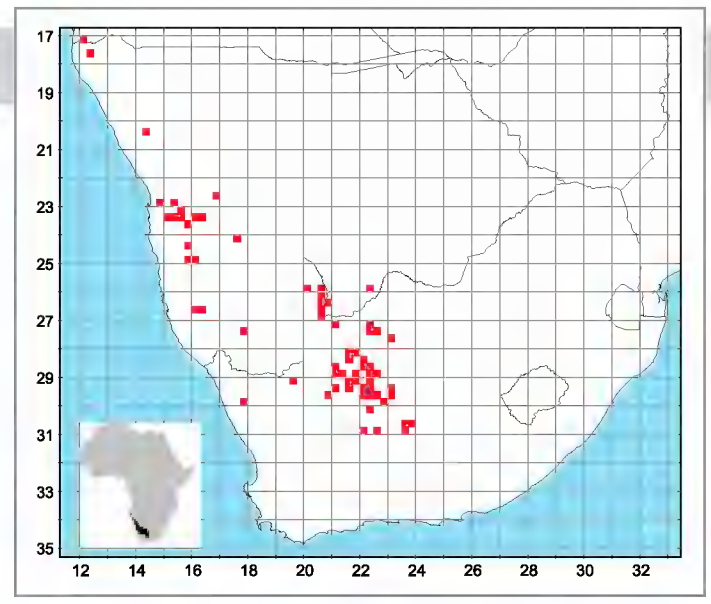
Global: LC
Endemic: RSA, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Scarabaeus pabulator*: 'Cape Colony (Calvinia)' [Northern Cape, South Africa].
Taxonomy: Accepted species.
Distribution: Centred on the S of the arid, late summer rainfall region, primarily in climate types III1 and III2 (Walter & Lieth 1964): NW South Africa, S Namibia; outlier occurrence at Nylsvlei requires validation (black square).
Locality data (mean ± SD, range): Altitude: 941 ± 166, 608–1 303 m; annual rainfall: 168 ± 85, 43–585 mm; annual temperature (max. + min. /2): 18.8 ± 1.2, 15.8–20.6°C (N=40).
Habitat: No adequate quantitative assessment; in Northern Cape: primarily recorded in arid Bushmanland (n=30 sites) rather than moister Karoo (n=7) or Kalahari (n=1); sampled from deep and stony sand (1.8/trap) and sandy loam (0.6/trap) in scrub and open shrubland.
Food types: No quantitative assessment; sampled to dung of pig and mixed cattle/sheep baits.
Temporal activity: Diurnal flight activity primarily in the late summer rainy season (Jan. to Mar.); other records may reflect a distribution extending to the edge of the winter rainfall region.
Ecoregions Namibia: S Namibian Savanna Woodlands (AT1316).
Bioregions South Africa: Centred on Bushmanland (NKb), margins of Upper Karoo (NKu) (Nama Karoo Biome).
Assessment rationale: EOO = 247 150 km^2 (minus the Limpopo Province record in a deep sand outlier at Nylsvlei – black square); although few of the known records lie within reserves, *S. pabulator* is widespread on farms in the Northern Cape, South Africa, that are used primarily for the grazing of domestic livestock and have undergone very little transformation; therefore, assessed as Least Concern (LC).
Conservation measures: Assessment of conservation status would be improved by a quantitative survey to determine the full EOO, AOO and ecological associations; it is necessary to determine if a bias to sandy soils reduces the potential AOO; protected within the boundaries of the Namib-Naukluft National Park, Namibia and the Riemvasmaak Community Conservancy, South Africa.

Scarabaeolus parvulus

(Boheman, 1860)



No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Ateuchus parvulus*: 'Regione fluvii Svakop' [Swakop River region, W central Namibia].

Taxonomy: Accepted species.

Distribution: Centred on the arid late summer rainfall region from the Northern Cape, South Africa, across extreme SW of Botswana plus S and NW Namibia to SW Angola.

Locality data (mean ± SD, range): Altitude: 991 ± 279, 47–1 809 m; annual rainfall: 196 ± 71, 27–367 mm; annual temperature (max. + min. /2): 18.5 ± 1.6, 14.1–21.2°C (N=108).

Habitat: No adequate quantitative assessment; in the Northern Cape: recorded at many study sites in SW Kalahari (26) and N Nama Karoo (49) primarily on deep or stony sand (3.6/trap; n=55), less in sandy loam (0.6/trap; n=19); DBRU collection records primarily from sand (1), sandy loam (1) in open vegetation: grassland (3), scrub/shrubland (8), open woodland (2).

Food types: No adequate quantitative assessment; in Botswana: sampled to pig (2) and cattle (4) dung; limited DBRU collection records from various dung types: cattle (3), wildebeest (1) donkey (1), horse (1), springbok (1), and carrion: dead dog (1).

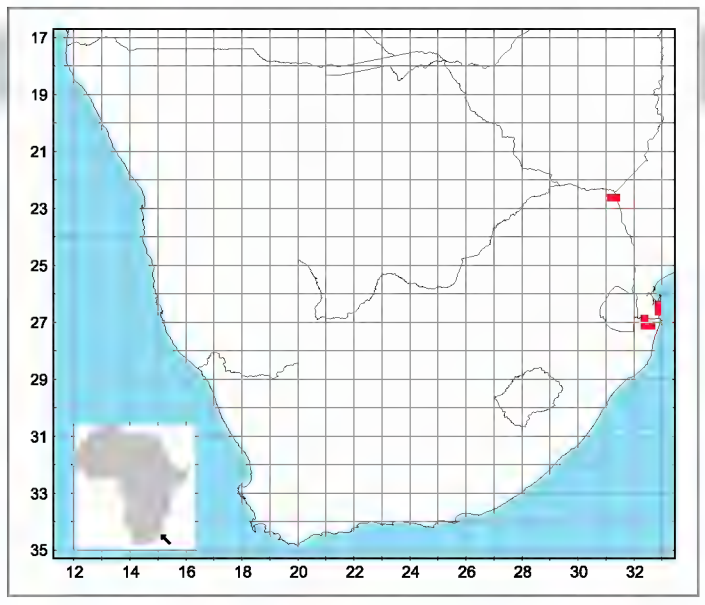
Temporal activity: Diurnal flight activity; recorded throughout the year (Oct. to Aug.), possibly because of a range extending from a seasonal rainfall system into the Namib Desert.

Ecoregions Namibia, Botswana: Nama Karoo (AT1314), Namib Desert (AT1315), Kaokoveld Desert (AT1310), Namibian Savanna Woodlands (AT1316), SW Kalahari Xeric Savanna (AT1309).

Bioregions South Africa: Centred on Kalahari Duneveld (SVkd), arid deep sands that dominate W Eastern Kalahari Bushveld (SVk) (Savanna Biome), N Upper Karoo (NKu), N Bushmanland (NKb) (Nama Karoo Biome).

Assessment rationale: EOO = 398 100 km^2; widespread across a little-transformed, arid region used primarily for the grazing of domestic livestock with some areas under conservation; also recorded on a wide variety of dung types; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by further quantitative data on ecological associations; in South Africa, officially protected only across a very small part of its range in Kgalagadi Transfrontier Park (South Africa, Botswana); also protected in the Namib-Naukluft Park (Namibia).



Scarabaeolus planipennis

(Davis & Deschodt, 2015b)

No synonyms (but see Taxonomy)

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Scarabaeus* (*Scarabaeolus*) *planipennis*: 'Maputo Elephant Reserve, Mozambique'.

Taxonomy: Accepted species; new species, *Scarabaeolus krugeri* (Zídek & Pokorný, 2018), is considered an unpublished synonym of *S. planipennis* (see Preamble).

Distribution: Known from coastal sands at the S tip of the Mozambique Coastal Plain; also inland sand outliers up the valley of the Limpopo River: South Africa, Mozambique.

Locality data (mean ± SD, range): Altitude: 92 ± 161, 0–475 m; annual rainfall: 685 ± 99, 482–773 mm; annual temperature (max. + min. /2): 22.5 ± 0.3, 22.4–23.4°C (N=12).

Habitat: On deep sand in Maputo Special Reserve, Mozambique: associated with grassland of saline pans (17) rather than forest patches (small (1), medium (0), large (0)); in Tembe and Sileza game reserves: associated with mixed woodland (19) rather than sand forest (3); Kruger National Park records all from sandveld.

Food types: No published quantitative data; cited as showing a bias to omnivore rather than herbivore dung.

Temporal activity: Diurnal flight activity during the summer rainy season (Oct. to Apr.).

Ecoregions Mozambique: Grassy sand patches in Maputaland Coastal Forest Mosaic (AT0119).

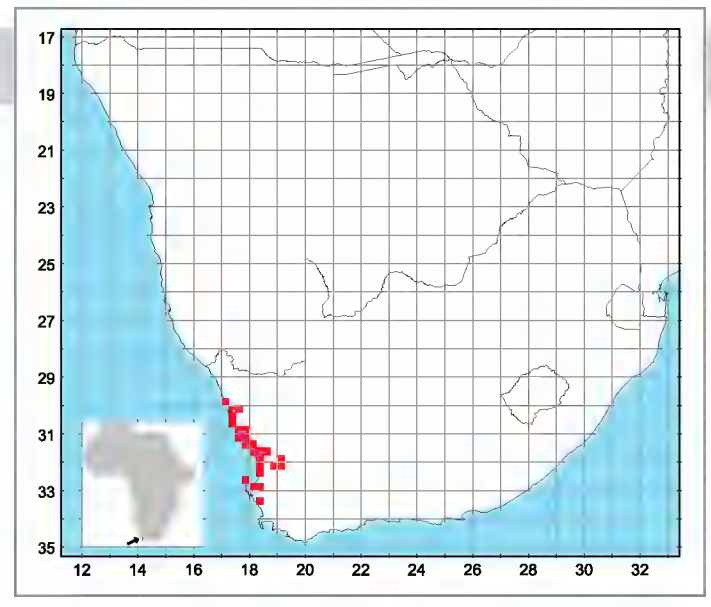
Bioregions South Africa: Vegetation units on deep sand: Nwambyia–Pumbe Sandy Bushveld (SVl 2), Tembe Sandy Bushveld (SVl 18), Cathedral Mopane Bushveld (SVmp 3) (Lowveld (SVl) and Mopane (SVmp), Savanna Biome); Maputaland Wooded Grassland (CB 2) (Indian Ocean Coastal Belt Biome (CB)).

Assessment rationale: EOO = 4 900 km^2 (may be underestimated); AOO would be even smaller as the species is probably a deep sand specialist in more open vegetation, but improved supporting data is required; although the AOO is potentially < 5 000 km^2 all known localities are found in conserved areas; therefore, not currently considered to be threatened; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by a quantitative survey of the S Mozambique Coastal Plain to better define the EOO, AOO and ecological associations; all known localities protected in the Kruger National Park plus Sileza and Tembe game reserves (South Africa) or the Maputo Special Reserve (Mozambique).

Scarabaeolus reichei

(Waterhouse, 1890) (but see Taxonomy)

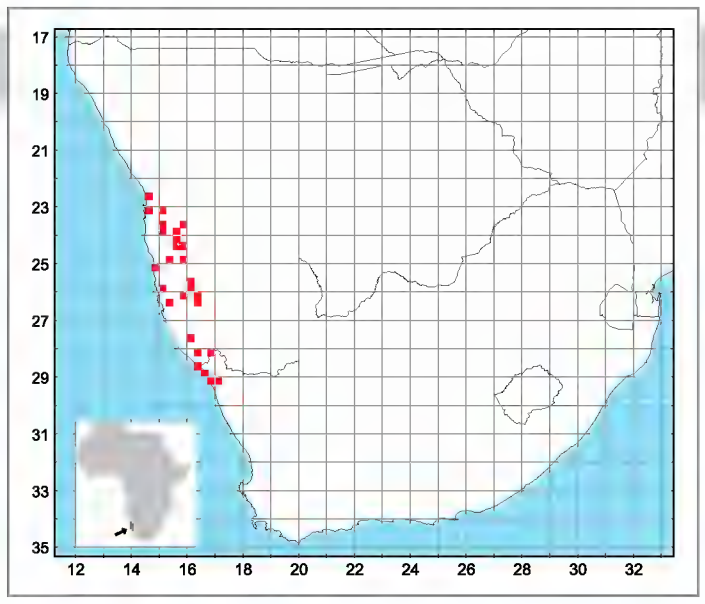


No synonyms

Global: LC (see IUCN Red List – DD as *Scarabaeus canaliculatus*
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Scarabaeus reichei*: 'Cape of Good Hope' [South Africa].
Taxonomy: Accepted species; recently revalidated from synonymy with *S. canaliculatus* Fairmaire, 1888; more recently, again incorrectly synonymised with *S. canaliculatus* (Fairmaire, 1888) by Zídek and Pokorný (2018), who did not see the lost type of *S. canaliculatus* or material of that species from southern Namibia (Namib Desert).
Distribution: Restricted to the arid West Coast in the winter rainfall region of South Africa with N range limits in Little Namaqualand; no overlap with the ranges of *S. fritschi* Harold, 1868 (Northern Cape interior, South Africa and S Namibia) or *S. canaliculatus* Fairmaire, 1888 (S Namib Desert, Namibia).
Locality data (mean ± SD, range): Altitude: 99 ± 84, 0–357 m; annual rainfall: 170 ± 52, 87–323 mm; annual temperature (max. + min. /2): 17.7 ± 0.8, 15.2–19.1°C (N=63).
Habitat: No adequate quantitative assessment; in Western Cape: sampled on deep sand in open shrubland (Modderrivier: 3) or very sandy loam in sparse grass (Groote Post: 16); DBRU collection records entirely from deep sand (6) in scrub (4) or crop fields (2).
Food types: No quantitative assessment; DBRU collection records from carrion (1 – dead fox) and several dung types: cattle (5), sheep (1).
Temporal activity: Diurnal flight activity recorded in the moist spring to dry early summer (Aug. to Dec.) and in moist autumn (Apr.).
Bioregions South Africa: Centred on Namaqualand Sandveld (SKs) (Succulent Karoo Biome); vegetation units in West Strandveld (FS), Sand Fynbos (FFd), margins of Sandstone Fynbos (FFs) (Fynbos Biome).
Assessment rationale: EOO = 12 500 km^2; relatively restricted range although it frequents both low profile natural scrub as well as disturbed vegetation, including fallow crop fields and dry grassland pastures on farms cleared of natural shrubs in the S of its range where there is from 35 to 70% transformation (FFd 4, FS 2, FS 3); perhaps less threatened than the many extreme, winter rainfall, shrubland specialists, although immigration into disturbed patches from natural vegetation cannot be ruled out; assessed as Least Concern (LC).
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; a small part of the range is protected in the coastal portion of the Namaqua National Park, which lies in the little-transformed (2%) Namaqualand Sandveld Bioregion (South Africa).



Scarabaeolus rubripennis

(Boheman, 1860) (but see Taxonomy)

No synonyms

Global: LC
Endemic: RSA, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Ateuchus rubripennis*: 'in regione fluvii Kuisip' [Kuiseb River region, W central Namibia].

Taxonomy: Accepted species, but southern populations in NW South Africa now separated as *Scarabaeolus lizleri* (Zídek & Pokorný, 2018).

Distribution: Centred on the main Namib Desert Dunefield, SW Namibia, and dunes straddling the Namibia/South Africa border.

Locality data (mean ± SD, range): Altitude: 594 ± 396, 1–1 655 m; annual rainfall: 56 ± 30, 1–132 mm; annual temperature (max. + min. /2): 16.0 ± 0.8, 13.5–17.5°C (N=35).

Habitat: No quantitative assessment; presumed to be specialised to deep sands of sparsely vegetated dunes with which most known localities coincide.

Food types: No quantitative assessment; attracted in abundance to pig dung.

Temporal activity: Diel flight periodicity unknown, but black pilosity is indicative of day-flying habits; recorded throughout the year (Apr. to Feb.) suggesting relatively aseasonal habits although this assessment is based on presence or absence rather than quantitative data.

Ecoregions Namibia: Namib Desert (AT1315), Succulent Karoo (AT1322).

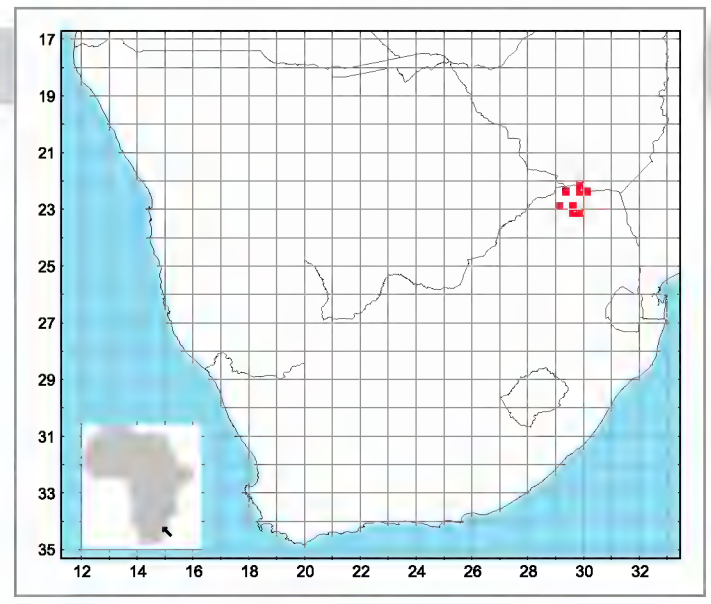
Bioregions South Africa: Vegetation unit: Richtersveld Coastal Duneveld (SKs 1) (Namaqualand Sandveld (SKs), Succulent Karoo Biome) (*S. lizleri*).

Assessment rationale: EOO = 55 500 km^2; widespread across an arid, lowland region that is mostly under official protection; no protection at the extreme southern margin of the species range in South Africa (now *S. lizleri*), which coincides with a vegetation unit (SKs 1) that is partially transformed (10%) by mining; nevertheless assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; predominantly protected in Namibia where most known localities lie within the Namib-Naukluft or Sperrgebiet national parks; protection within South Africa would also be desirable, particularly as this population has now been separated as the new species, *S. lizleri*.

Scarabaeolus soutpansbergensis

(Deschodt & Davis 2015b)



No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Scarabaeus* (*Scarabaeolus*) *soutpansbergensis*: 'Soutpansberg' [mountain range, Limpopo Province, South Africa].
Taxonomy: Accepted species.
Distribution: Dry savanna just to the S of the Soutpansberg and to the N in the Limpopo Valley, Limpopo Province, South Africa.
Locality data (mean ± SD, range): Altitude: 741 ± 220, 429–1 020 m; annual rainfall: 434 ± 128, 306–653 mm; annual temperature (max. + min. /2): 21.2 ± 1.6, 19.2–23.4°C (N=10).
Habitat: No quantitative assessment; holotype recorded on deep sand in open mopane woodland.
Food types: No quantitative assessment.
Temporal activity: Diel flight periodicity unknown, but presumed to be diurnal on the basis of black pilosity; recorded during the summer rainy season (Dec., Feb.).
Bioregions South Africa: Vegetation units: Musina Mopane Bushveld (SVmp 1), Limpopo Ridge Bushveld (SVmp 2), Roodeberg Bushveld (SVcb 18), N Makhado Sweet Bushveld (SVcb 20) (Mopane (SVmp) and Central Bushveld (SVcb) (Savanna Biome).
Assessment rationale: EOO = 5 100 km^2 (underestimated); relatively poorly known species with a known EOO hardly more than 5 000 km^2; recorded from four vegetation units that are 18–27% transformed (SVcb) or only 1–2% transformed (SVmp); little known concerning species attributes; assessed as Data Deficient (DD).
Conservation measures: To assess conservation status, a more extensive quantitative survey is required to determine the full EOO, AOO, and ecological associations; protected within the Blouberg and Musina nature reserves (South Africa).

Genus *Scarabaeus* Linnaeus, 1758

Type species and designation: *Scarabaeus sacer* Linnaeus, 1758, by subsequent designation (Hope 1837).

Synonyms:
= *Heliocantharus* Macleay, 1821 (*pars*): *Scarabaeus sacer* Linnaeus, 1758, by original designation.
= *Ateuchus auctorum* (not Weber, 1801).
= *Sebasteos* Westwood, 1847: *Sebasteos galenus* Westwood, 1847, by original designation.
= *Neateuchus* Gillet, 1911: *Ateuchus proboscideus* Guérin-Meneville, 1844, by original designation.
= *Drepanopodus* Janssens, 1940: *Ateuchus costatus* Wiedemann, 1823, by monotypy.

Last review: Entire genus reviewed by zur Strassen (1967) with updated checklist (Zídek 2004); many of the species listed by Zídek (2004) transferred to *Scarabaeolus* (Balthasar, 1965b), after it was raised to genus level by Moretto (2016b); review of subgeneric affiliations (Zídek & Pokorný 2011), mainly Palaearctic species, now all raised to generic status (Ziani & Gudenzi 2012).

The designation of *Scarabaeus hercules* Linnaeus, 1758 (Subfamily Dynastinae), as the type species of the genus (Latreille 1810) takes precedence over the subsequent designation of *Scarabaeus sacer* Linnaeus, 1758 (Subfamily Scarabaeinae) as the type species (Hope 1837). However, on the basis of prevailing usage and to avoid confusion, it has been proposed that *S. sacer* should be conserved as the type species of *Scarabaeus*. This currently forms part of Open Case 3590 submitted for a ruling from the International Commission of Nomenclature (Krell et al. 2012).

In its strictest sense as a genus of the subfamily Scarabaeinae, *Scarabaeus* Linnaeus, 1758, is centred on the Afrotropical and S Palaearctic regions extending into the W edge of the Oriental region. A recent revision divided the Palaearctic and Oriental members of the genus into four subgenera (Zídek & Pokorný 2008) now all raised to generic level (Ziani & Gudenzi 2012). One of these genera, *Escarabaeus* Zídek & Pokorný, 2011, also occurs S of 15°S in southern Africa, where it is represented by at least two species. However, affiliations have not been formally assessed for the remaining 31 (or 33) southern African species currently listed as *Scarabaeus*. A phylogeny (Barbero et al. 1998) suggests that at least some of these species would belong to different genera to those described for the Palaearctic. However, pending further study, they remain listed as *Scarabaeus* species (importantly, in the 2019 version of the Catalogue of Life, *S. hottentorum* Péringuey, 1901 and *S. savignyi* Macleay, 1821, are transferred to the genus, *Ateuchetus* Bedel, 1892).

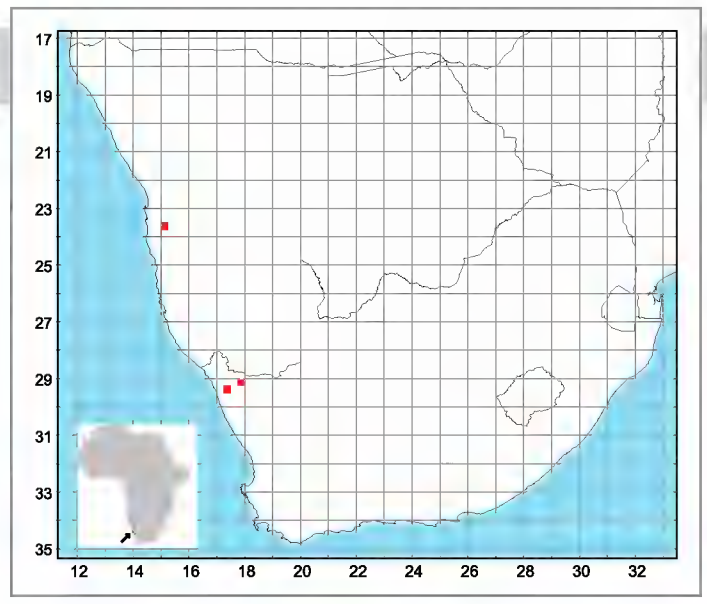
Cited synonyms are for pterous genera and have been reduced from those listed by Zídek and Pokorný (2004) according to the generic-level divisions proposed by Ziani and Gudenzi (2012). They may change, again, after revision of generic-level affiliations shown by the 31 (or 33) southern African species. As three out of five flightless taxa have been revalidated at generic level, listed synonyms do not include the two remaining flightless taxa from Madagascar that are still officially synonymised with *Scarabaeus*: *Neomnematium* Janssens, 1938a, *Madateuchus* Paulian, 1953.

Patterns of species distribution in southern Africa have been divided into four centres. One was centred on the SW Kalahari plus Namib Desert (1 sp.) plus W coast of South Africa (1), just the N Namib (1), S Namib plus Namaqualand (1), Namaqualand (1), W coast of South Africa (2) or SW Western Cape (1). Another was centred on the drier Highveld and N Namibia (2), Highveld to Upper Karoo (1), just N Highveld (2) or Karoo (1). The third was centred on moist NE Highveld (2), Maputaland (1), NE Highveld to S Cape (1), or just the S Cape (1). The fourth was centred on savanna, all regions (2), just E and W (1), W (1), or E (5), also, E and Kalahari (1) or just Kalahari (1).

The ranges of about half of the species wholly or partly coincide with drier regions in which there has been relatively little habitat transformation. A few show ranges that are restricted to areas of high transformation. A total of 17 species were assessed as Least Concern (LC), one was assessed as Near Threatened (NT) and the remainder (13) as Data Deficient (DD). Several of the latter may deserve an IUCN threat category, particularly those occupying small known EOOs in areas of high transformation.

Scarabaeus alienus

Péringuey, 1901

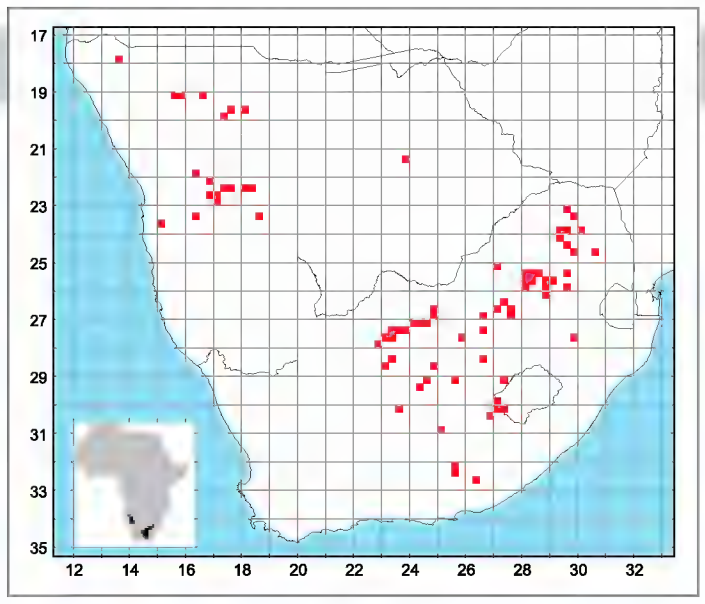


No synonyms

Global: DD
Endemic: RSA, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: Cited as 'not known'.
Taxonomy: Accepted species.
Distribution: Extremely arid range; records from NW South Africa occur at the northern limits of climate type III1 (Walter & Lieth 1964); unknown if there is a continuous distribution between N and S records assuming that the Namibian record in climate type III2 is valid.
Locality data (mean ± SD, range): Altitude: 574 ± 178, 400–755 m; annual rainfall: 65 ± 41, 18–90 mm; annual temperature (max. + min. /2): 17.2 ± 0.8, 16.7–18.1°C (N=3).
Habitat: No quantitative assessment; DBRU collection records from sand (1) and sandy loam (1) in scrub (2).
Food types: No quantitative assessment; DBRU collection records from dung of horse (1) and donkey (1).
Temporal activity: Diurnal flight activity observed during daytime under dry, sunny conditions; shows spring activity (Sept.) in the winter rainfall region of South Africa.
Ecoregions Namibia: Namib Desert (AT1315).
Bioregions South Africa: Richtersveld (SKr) (Succulent Karoo Biome).
Assessment rationale: EOO = 18 000 km^2; known from only three widely separated localities; rarity possibly an artefact of the dry conditions under which the collections were made; two South African records occur outside of protected areas; assessed as Data Deficient (DD).
Conservation measures: Conservation status cannot be assessed from current data; a quantitative survey is required to ascertain the full EOO, AOO and ecological associations; in South Africa, not currently recorded in Richtersveld National Park; protected in Namibia within the Namib-Naukluft Park assuming that the record from Gobabeb is valid.



Scarabaeus ambiguus

(Boheman, 1857)

= *Actinophorus leei* Shipp, 1896b
= *Scarabaeus viator deceptor* Péringuey, 1901 (*pars*)

Global: LC (see IUCN Red List – LC)
Endemic: RSA, Botswana, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Ateuchus ambiguus*: 'Caffraria meridionali' [southern Africa]; *A. leei*: 'Swan River, West Australia' [locality labelling error]; *S. viator deceptor*: '(Cape Town), Transvaal (Potchefstroom), Bechuanaland (Kanye)' [Potchefstroom, North-West Province, South Africa; Kanye, Botswana], [Cape Town type locality would be an error = *S. viator* Péringuey, 1901].

Taxonomy: Accepted species.

Distribution: Drier W and NW highveld, South Africa, and drier N upland plateau, Namibia; rare occurrence at Gobabeb in Namib Desert; also rare in the Botswana Kalahari, which essentially represents a disjunction in the range; SW edge of range approaches that of the very close relative, *S. viator* Péringuey, 1901.

Locality data (mean ± SD, range): Altitude: 1 323 ± 247, 424–2 074 m; annual rainfall: 509 ± 156, 22–833 mm; annual temperature (max. + min. /2): 18.0 ± 1.7, 12.2–22.6°C (N=106).

Habitat: In Gauteng bushveld: strong bias to sandy clay loam (38) compared to deep sand (5), and to grassland (38) compared to open woodland (5) and shaded thicket (0); similar vegetation bias in Ezemvelo Nature Reserve (now Telperion): grass (105), open woodland (10); conflicting soil type results in open woodland at Leeuwfontein Game Reserve: loamy sand (1 595), sandy loam (145), stony sandy loam (857); DBRU collection records from sand (18), sandy loam (22), sandy clay loam (7) in grassland/pasture (27), scrub/shrubland (9), open woodland (8).

Food types: No quantitative assessment; DBRU collection records mainly from dung of cattle (40), also horse (2), zebra (3).

Temporal activity: Diurnal flight activity during the summer rainy season (Oct. to May); in Gauteng bushveld: primarily active in the early morning after substantial rainfall.

Ecoregions Namibia, Botswana: Angolan Mopane Woodlands (AT0702), NW Kalahari Xeric Savanna (AT1309), Kalahari Acacia-Baikiaea Woodlands (AT0709), margins of two other ecoregions.

Bioregions South Africa: Eastern Kalahari Bushveld (SVk), higher SE and E Central Bushveld (SVcb) (Savanna Biome); Dry Highveld Grassland (Gh), W margins Mesic Highveld Grassland (Gm) (Grassland Biome); scattered records at NE margins of Upper Nama Karoo (NKu) (Nama Karoo Biome).

Assessment rationale: EOO = 371 530 km^2 (main range; excludes three outliers); widespread on various soil types with a bias to open grassland habitat that is dominant over much of its upland range; on basis of wide occurrence and abundance in several reserves, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by further quantitative data to resolve conflicts between existing results for ecological associations and lack of data on effects of habitat transformation; protected in various national parks and reserves including Telperion, Leeuwfontein (South Africa), Etosha (Namibia).

Scarabaeus basuto

zur Strassen, 1962

= *Scarabaeus natalensis* zur Strassen, 1962
= *Scarabaeus ambiguus* (Boheman, 1857) *sensu* Péringuey, 1901

Global: LC
Endemic: RSA, Lesotho

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *S. basuto*: 'Molokoolu' (= Mohlokulu), Mohales Hoek Distrikt, Basutoland' [Mohlokulu, Lesotho]; *S. natalensis*: 'Newcastle, Natal' [KwaZulu-Natal, South Africa]; *S. ambiguus sensu* Péringuey: 'Cape Colony (Cape Town), Transvaal (Potchefstroom), Natal (Estcourt)' [South Africa: Western Cape, North-West Province, KwaZulu-Natal; see Taxonomy section].

Taxonomy: *S. natalensis* was recently synonymised with *S. basuto* since a principal character forms a NE–SW cline whereas other characters occur asymmetrically at end points on the cline; synonymy of *S. ambiguus sensu* Péringuey with *S. natalensis* requires further investigation on the basis of cited localities, particularly Cape Town.

Distribution: Ranging along the SE Highveld: South Africa, Lesotho; recorded from Grassland Biome in the NE to Upper Nama Karoo in the SW; map marks the type localities of the two species recognised by zur Strassen (*S. basuto*: black; *S. natalensis*: blue).

Locality data (mean ± SD, range): Altitude: 1 460 ± 268, 1 065–2 562 m; annual rainfall: 455 ± 214, 221–958 mm; annual temperature (max. + min. /2): 14.8 ± 1.5, 8.4–17.3°C (N=63).

Habitat: No quantitative assessment; in the Northern Cape: primarily from Upper Karoo (39 out of 68 study sites) on sandy loam (8.8 per sample), sand/loamy sand (3.3 per sample); DBRU collection records biased to E localities: sand (4), sandy loam (4), sandy clay loam (3) in grassland/pasture (8), shrubland (2).

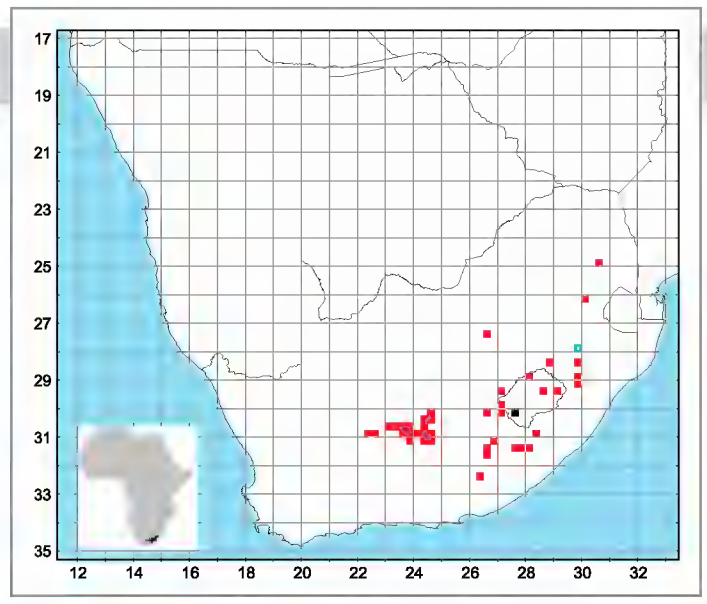
Food types: No quantitative assessment; DBRU collection records from dung of cattle (12), sheep (2).

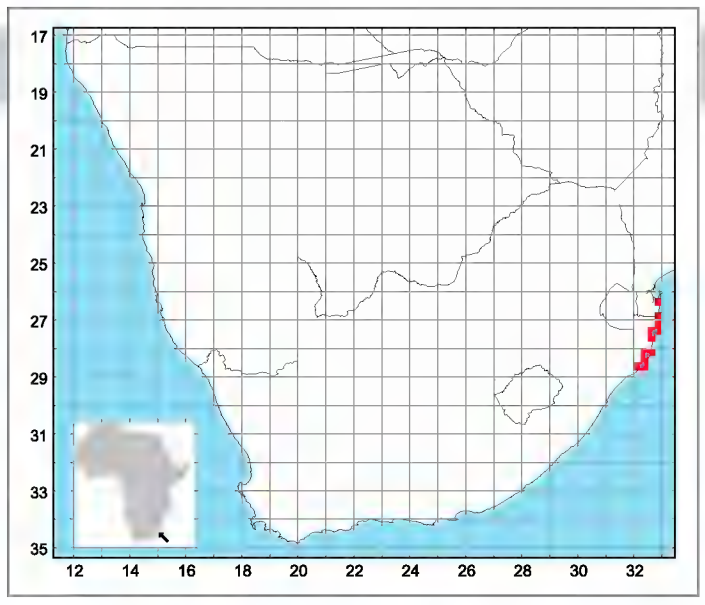
Temporal activity: Diurnal flight activity in the summer rainy season (Oct. to Mar.) with a bias to late summer (Feb., Mar.) in Upper Karoo.

Bioregions South Africa: Highland edges Mesic Highveld Grassland (Gm), Drakensberg Grassland (Gd), Sub-Escarpment Grassland (Gs) (Grassland Biome); N Upper Karoo (NKu) (Nama Karoo Biome).

Assessment rationale: EOO = 134 360 km^2; molecular analysis would be useful to support synonymy of *S. natalensis* with *S. basuto*; whether considered as one or two species, currently assessed as Least Concern (LC) on basis of limited habitat transformation over most of the large, combined, highland range.

Conservation measures: Assessment of conservation status would be improved by resolution of taxonomic issues and quantitative data on ecological associations, particularly, possible effects of habitat transformation in E of range; not currently known from any protected area.





Scarabaeus bornemisszai

zur Strassen, 1980

No synonyms

Global: NT (see IUCN Red List – NT)

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'St Lucia Estuary, coastal dune forest' [KwaZulu-Natal, South Africa].

Taxonomy: Accepted species.

Distribution: Restricted to the Maputaland Centre of Endemism in NE KwaZulu-Natal (South Africa) and SE Mozambique.

Locality data (mean ± SD, range): Altitude: 12 ± 24, 0–85 m; annual rainfall: 875 ± 98, 743–1 011 mm; annual temperature (max. + min. /2): 22.0 ± 0.3, 21.4–22.4°C (N=23).

Habitat: In Maputo Special Reserve: mostly in coastal-fringing dune forest (16.8/trap); uncommon in warmer, inland sand forest (0.2); virtually absent from grassland on fossil lagoons (0.04); across a post-mining vegetation succession at Richards Bay: present only in dense woodland (9–20 yr) (15) and natural dune forest (71), absent from unshaded shrub/grassland (0–8 yr) and open woodland (21–33 yr); DBRU collection records all from sand (2) in forest (9).

Food types: No quantitative assessment; DBRU collection records from human (1) and a mixture of human and cattle dung (1); sampled to pig dung and a mixture of pig and cattle dung.

Temporal activity: Diurnal flight activity during the summer rainy season (Oct. to May) with some activity in spring (Aug.).

Ecoregions Mozambique: Maputaland Coastal Forest Mosaic (AT0119).

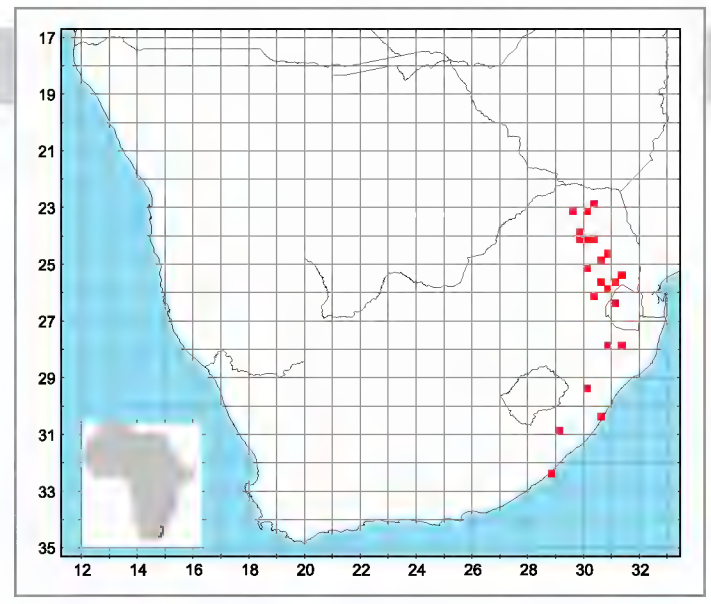
Bioregions South Africa: Vegetation unit: Centred on deep sands, Northern Coastal Forest (FOz 7) (Forest Biome (FO) encompassed by Indian Ocean Coastal Belt Biome (CB)).

Assessment rationale: EOO = 3 250 km^2 comprising a narrow range along 325 km of coastline; AOO much smaller, primarily restricted to coastal dune forest patches; in South Africa, 50 km of coastline is mined for titanium-bearing sands; 185 km is protected as a World Heritage Site, which includes 68% of the vegetation unit (FOz 7); assessed as Near Threatened (NT) although currently well protected.

Conservation measures: Conservation status is dependent on continuing protection of existing reserves containing dune forest patches, including iSimangaliso Wetland Park (World Heritage Site) (South Africa) and Maputo Special Reserve (Mozambique); it would be useful to monitor status of the species in the mined area N of Richards Bay, of which a third is being permitted to regenerate as secondary forest; monitoring of illegal clearance and use of forest patches would also be useful.

Scarabaeus caffer

(Boheman, 1857)

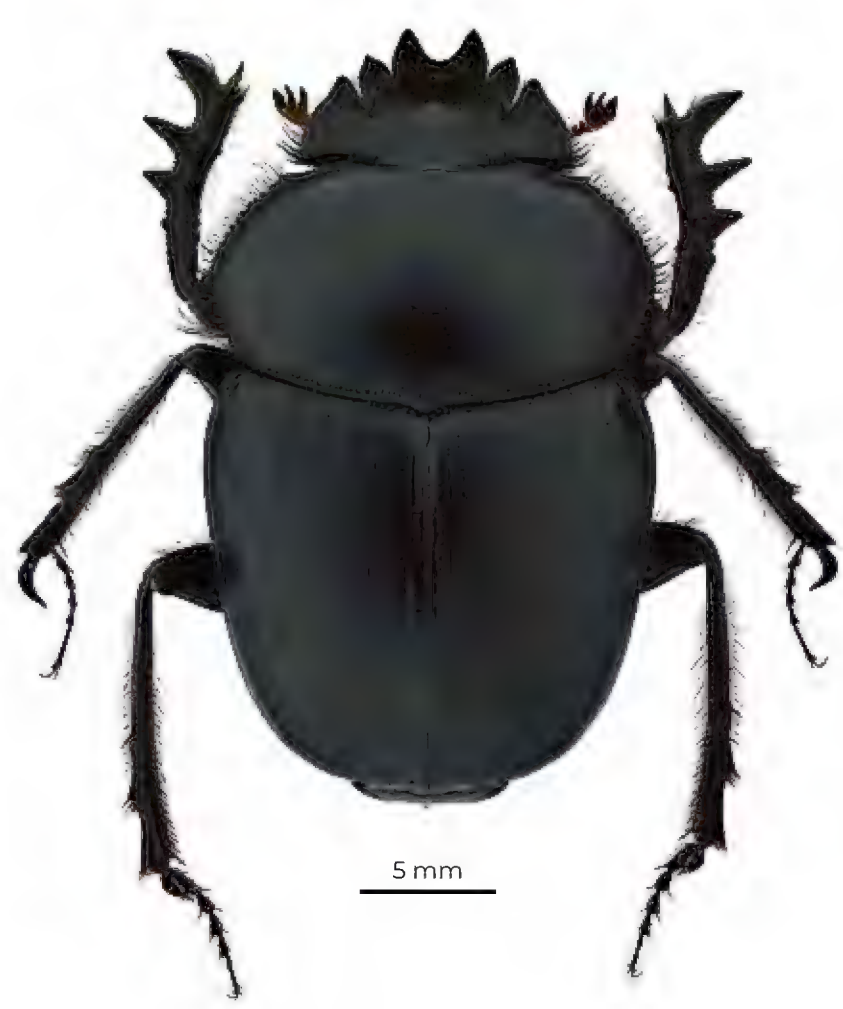


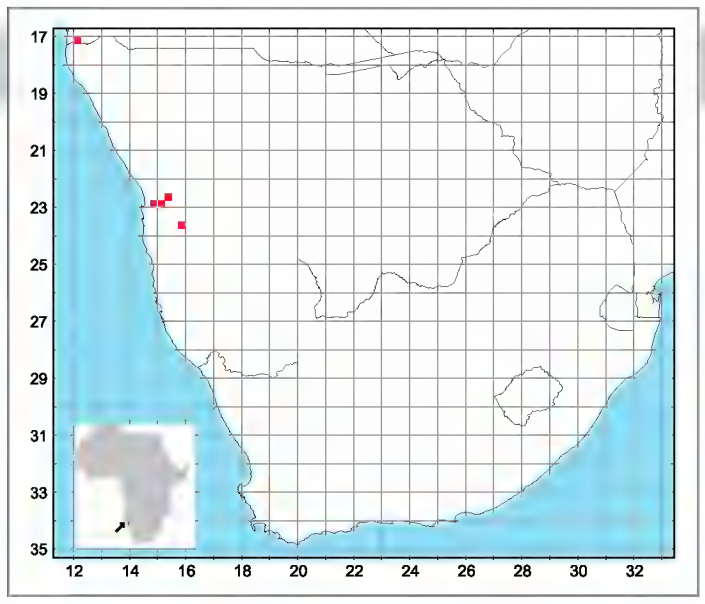
No synonyms

Global: LC (see IUCN Red List – DD)
Endemic: RSA, Eswatini

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Ateuchus caffer*: 'Caffraria tota passim' [everywhere, all SE South Africa].
Taxonomy: Accepted species.
Distribution: Centred in moist highlands along the upper edge of the E escarpment, NE South Africa, with a distribution southwards that descends to the coastline in the NE Eastern Cape; also reported from Eswatini; Zimbabwe report requires validation.
Locality data (mean ± SD, range): Altitude: 1 214 ± 469, 0–2 005 m; annual rainfall: 891 ± 130, 594–1 157 mm; annual temperature (max. + min. /2): 16.7 ± 2.3, 12.5–21.4°C (N=29).
Habitat: On finer-grained soils near Carolina: present in natural *Themeda*-dominated grassland (5), absent from fallow crop fields and improved Kikuyu pasture; at Wolkberg (1 400 m): much less abundant in forest (9) than adjacent grassland (299); one DBRU collection record from sandy clay loam in grassland.
Food types: At Wolkberg (1 400 m): equally abundant on dung of pig (154) and cattle (154); one DBRU collection record from cattle dung.
Temporal activity: Diurnal flight activity, primarily in the summer rainy season (Oct. to Apr.).
Bioregions South Africa: Montane or mistbelt vegetation units: E Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs) (Grassland Biome); S Indian Ocean Coastal Belt Biome (CB); vegetation unit: moist S edge, Soutpansberg Mountain Bushveld (SVcb 21) (Central Bushveld (SVcb), Savanna Biome).
Assessment rationale: EOO = 70 500 km^2; probably threatened by pasture improvement, cultivation and creation of forest plantations in parts of its range; transformation: 0–70% in the N (E Gm), 3–50% in the S (Gs); However, re-assessed as Least Concern (LC) due to the large EOO, abundance in one reserve, and ready attraction to dung of domestic livestock.
Conservation measures: Assessment of conservation status would be improved by a quantitative survey of farmland and reserves across the known range; an investigation of soil associations and its abundance in transformed vs natural grassland would be particularly useful; protected and abundant in Lekgalameetse Nature Reserve, Wolkberg.





Scarabaeus cognatus

Péringuey, 1901

No synonyms

Global: DD
Endemic: Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Damaraland (Salem)' [Namibia].
Taxonomy: Accepted species; one of three elongate species, until recently, classified in the genus *Drepanopodus* Janssens, 1940.
Distribution: Currently known from two disjunct, arid, lowland, population centres below the W escarpment, one near the coastline in N Namibia; one in the central Namib Desert in Namibia; record from the Cape, South Africa, would represent confusion with the closely related *S. proximus* Péringuey, 1901.
Locality data (mean ± SD, range): Altitude: 531 ± 244, 283–594 m; annual rainfall: 77 ± 50, 29–157 mm; annual temperature (max. + min. /2): 17.7 ± 0.6, 16.8–18.3°C (N=5).
Habitat: No quantitative assessment; collected from the gravel plains of the Namib Desert where there is very sparse scrub cover.
Food types: No quantitative assessment; sampled to pig dung near Solitaire, central Namibia.
Temporal activity: Diurnal flight activity in the late summer rainy season (Feb. to Apr.); also recorded after light rainfall in June.
Ecoregions Namibia: Below escarpment: W Namibian Savanna Woodlands (AT1316), Namib Desert (AT1315), Kaokoveld Desert (AT1310).
Assessment rationale: EOO = 18 345 km^2; known only from two ultra-arid desert centres; some sampled localities lie within an area scheduled for mining; however, most of potential EOO used for grazing of livestock or under conservation; a poorly known species; therefore, assessed as Data Deficient (DD).
Conservation measures: A quantitative survey of the full EOO, AOO and ecological associations is required before an assessment of conservation status may be made; this should investigate the possibility of continuous distribution from the S range limits in the Namib-Naukluft Park along the protected Skeleton Coast to and beyond the northernmost known locality on the Angolan border.

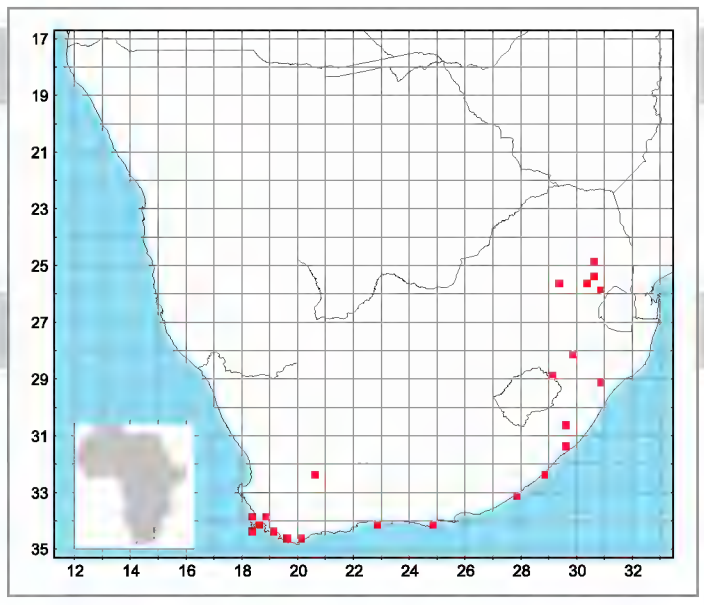
Scarabaeus convexus

(Hausmann, 1807)

= *Ateuchus laevis* Thunberg, 1818

Scarabaeus spretus

zur Strassen, 1962



Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Ateuchus convexus*: Not stated, but collector (Friedrich Hesse) was based in Cape Town [Western Cape, South Africa]; *A. laevis*: 'majorem horum partem in capite bonae spei collegi' [amongst material mostly collected in the Cape of Good Hope, South Africa]; *S. spretus*: 'Umgebung Kapstadt' [surroundings of Cape Town].

Taxonomy: Currently, two accepted species, presumably, sharing type localities in the vicinity of Cape Town (*S. convexus* is described together with Western Cape endemics: *S. suri*, *S. rugosus* (both Hausmann, 1807)); apparently no consistent differences between individuals identified as *S. convexus* (S Cape to Mpumalanga) or *S. spretus* (W and S Cape); further study required.

Distribution: Coastal localities from Western Cape (winter rainfall) to KwaZulu-Natal and highlands of E escarpment of Mpumalanga in the NE (both summer rainfall).

Locality data (mean ± SD, range): N localities (8): Altitude: 1 424 ± 412, 864–2 274 m; annual rainfall: 828 ± 113, 684–1 022 mm; annual temperature (max. + min. /2): 15.6 ± 2.2, 10.6–17.4°C (N=9). S localities (14): Altitude: 234 ± 439, 0–1 542 m; annual rainfall: 510 ± 204, 201–955 mm; annual temperature (max. + min. /2): 16.5 ± 2.2, 11.7–19.5°C (N=15).

Habitat: On Cape Peninsula (*S. spretus*): sampled on deep sands in dense, low cover of *Restio*-dominated fynbos shrubland (2–3 yr since burning) (183 individuals), also, open cover but higher profile fynbos (9–10 yr since burning) (84), few on nearby transformed habitat comprising low, dense cover of Kikuyu grass (3); also recorded from sandy loam and sandy clay loam in forest and highland grassland.

Food types: No quantitative assessment; sampled to dung of cattle (*S. spretus*, *S. convexus*) and humans (*S. convexus*).

Temporal activity: Diurnal flight activity, mostly at similar levels of abundance from spring till autumn in winter rainfall region on Cape Peninsula (Aug.–Apr.); active during summer in the bimodal and summer rainfall regions (Oct.–Mar.).

Bioregions South Africa: In S: Southwest Fynbos (FO 2), Karoo Renosterveld (FO 9) (Fynbos Biome); Albany Thicket (AT), Indian Ocean Coastal Belt (CB) biomes; In N: Sub-Escarpment Grassland (Gs), Mesic Highveld Grassland (Gm) (Grassland Biome).

Assessment rationale: EOO = 45 980 km²; both names used interchangeably for populations in S Cape; *S. convexus* used for NE populations and *S. spretus* for those in extreme W Cape, even though both names are represented by types from the same general locality around Cape Town; may comprise a single species; does not show marked seasonal adaptation to winter rainfall on Cape Peninsula where it is active throughout summer; not currently threatened in SW or NE; assessed as Data Deficient (DD) owing to nomenclatural problems.

S. convexus

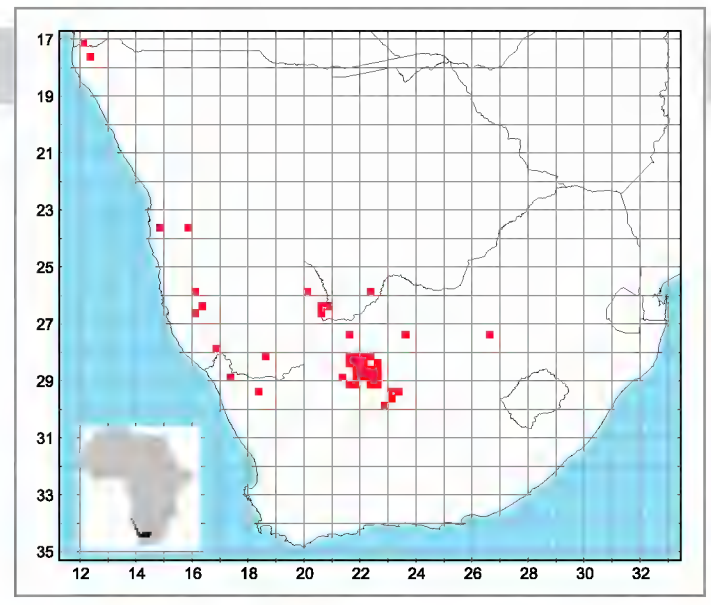
S. spretus

Scarabaeus convexus & *S. spretus* (continued)

Conservation measures: Before an assessment may be made of conservation status, nomenclatural problems need to be resolved; quantitative data on ecological associations are also required; SW populations protected in Cape of Good Hope Nature Reserve, NE populations in uKhahlamba Drakensberg Park (World Heritage Site).

Scarabaeus costatus

(Weidemann, 1823)



No synonyms

Global: LC (see IUCN Red List – LC)
Endemic: RSA, Botswana, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Ateuchus costatus*: 'Prom. bon. sp.' [Cape of Good Hope, South Africa]; some references cite type locality as Orange [River] whose lower reaches are within the known range.

Taxonomy: Accepted species; one of three elongate species, until recently, included in the genus *Drepanopodus* Janssens, 1940.

Distribution: Hot, arid, deep sands centred on the SW Kalahari and areas bordering the Namib Desert: NW South Africa, SW Botswana, W Namibia.

Locality data (mean ± SD, range): Altitude: 1 023 ± 195, 283–1 356 m; annual rainfall: 225 ± 78, 9–555 mm; annual temperature (max. + min. /2): 18.9 ± 1.2, 14.2–21.2°C (N=73).

Habitat: No adequate quantitative assessment; in Northern Cape: mostly restricted to SW Kalahari (5.34/trap), virtually absent from Bushmanland and Upper Karoo; in SW Kalahari: strong bias to deep sand (6.7, n=69), less on sandy loam (2.8, n=25), sandy clay loam (0, n=3); DBRU collection records from sand (9) in open vegetation: grassland (2), scrub (5), shrubland (2).

Food types: In Botswana: bias to dung of omnivores (pig: 42), less so to ruminant herbivores (cattle: 19, sheep: 4), absent from monogastric herbivore dung (elephant) and carrion (chicken livers); DBRU collection records on various dung types: human (1), horse (1), donkey (1), cattle (3).

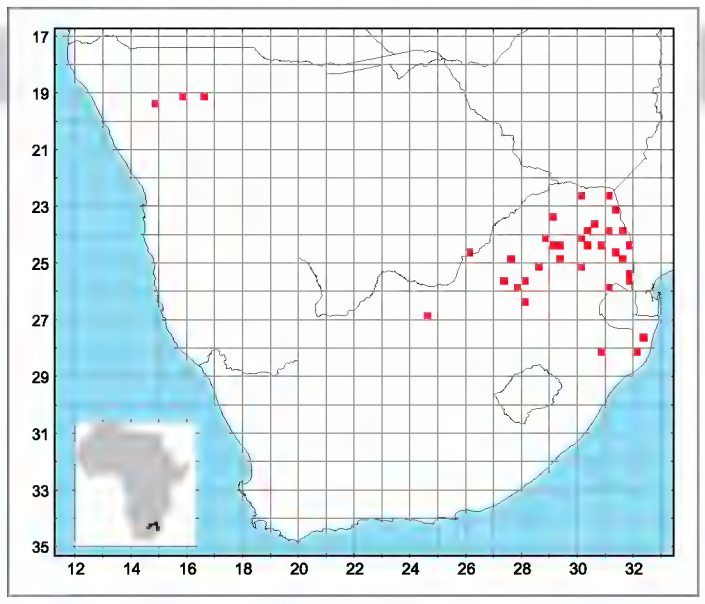
Temporal activity: Diurnal flight activity in the late summer rainy season (Dec. to Apr.); sensitive to movement, fly away if disturbed.

Ecoregions Namibia, Botswana: Nama Karoo (AT1314), S Kalahari Xeric Savanna (AT1309), Namibian Savanna Woodlands (AT1316), Namib Desert (AT1315), Kaokoveld Desert (AT1310).

Bioregions South Africa: Centred on Kalahari Duneveld (SVkd), W Eastern Kalahari Bushveld (SVk) (Savanna Biome); marginal occurrence in four adjoining bioregions.

Assessment rationale: EOO = 298 810 km^2; widespread in an arid, little-transformed region used primarily for conservation or grazing of domestic livestock on farm rangeland; AOO probably influenced by specialisation to sandy soils, but quantitative support required; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on soil associations; protected in Kgalagadi Transfrontier Park (South Africa/Botswana), Sperrgebiet and Namib-Naukluft national parks (Namibia).



Scarabaeus deludens

zur Strassen, 1961a

No synonyms

Global: LC (see IUCN Red List – LC)
Endemic: RSA, Botswana, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Roodeplaat, 24 km nö. Pretoria, Transvaal, ca. 1 300 m' [Roodeplaat, near Pretoria, Gauteng, South Africa].

Taxonomy: Accepted species; habitus close in appearance to *Escarabaeus satyrus* (Boheman, 1860), but aedeagus differs radically.

Distribution: Finer-grained soils in open shrub/woodland savanna; N South Africa, NE Botswana, N Namibia; unclear if distribution is truly disjunct to E and W of Kalahari deep sands due to association with finer-grained soils; citations from Zimbabwe and, particularly, Tanzania require validation.

Locality data (mean ± SD, range): Altitude: 795 ± 432, 55–1 588 m; annual rainfall: 610 ± 136, 314–900 mm; annual temperature (max. + min. /2): 20.4 ± 2.0, 16.5–23.6°C (N=40).

Habitat: No quantitative assessment; limited DBRU collection records from finer-grained soils, sandy clay loam (2), clay (2), in mopane shrubland (2).

Food types: No quantitative assessment; limited DBRU collection records from dung of elephant (3), cattle (1).

Temporal activity: Flight activity during darkness in the summer rainy season (Oct. to Apr.); attracted to light.

Ecoregions Namibia: S Angolan Mopane Woodlands (AT0702), margins of two other ecoregions.

Bioregions South Africa: Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome); marginal in three other bioregions.

Assessment rationale: EOO = 186 900 km^2 (possibly underestimated); AOO probably smaller due to association with finer-grained soils although quantitative support is required; assessed as Least Concern (LC) owing to widespread occurrence in farmland and reserves, although essentially Data Deficient (DD) owing to paucity of ecological association data.

Conservation measures: Assessment of conservation status would be much improved by quantitative data on ecological associations, particularly testing for soil type specialisation; protected in Kruger National Park (South Africa), Etosha National Park (Namibia).

Scarabaeus ebenus

(Klug, 1855)

= *Scarabaeus politifrons* Fairmaire, 1887
= *Scarabaeus sericeipennis* Fairmaire, 1887
= *Scarabaeus glabratus* Kolbe, 1895

Scarabaeus interstitialis

(Boheman, 1857)

No synonyms

Global: DD (for *S. ebenus*, see IUCN Red List – DD)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Ateuchus ebenus*: 'Inhambane' [central coast of Mozambique]; *S. politifrons*: 'Ouebbi' [Somalia]; *S. sericeipennis*: 'Kibanga' [Democratic Republic of the Congo (DRC)]; *S. glabratus*: 'Witu' [NE Kenya coast]. As *Ateuchus interstitialis*: 'Caffraria Interiore' [South African interior].

Taxonomy: Both accepted species, but treated together as aedeagi are identical and morphological characteristics represent a cline from the SE coastline onto the NW uplands of South Africa; synonyms of *S. ebenus* and records of both species require re-assessment.

Distribution: Typical *S. ebenus* are characterised by scattered fine pits on prothoracic disc and elytra: NE to S coast (Mozambique), Zambezi Valley (Zimbabwe, Botswana) (black squares); validation required for Tanzania, Namibia records and Somalia, Kenya synonyms of *S. ebenus*; Democratic Republic of the Congo (DRC) synonym and Ethiopia record are probably errors; on Pumbe Sands, NE lowlands, South Africa (arrowed): pits on the disc are largely similar to *S. ebenus*; however, to the S: pits on the disc are often larger and grade into typical *S. interstitialis* on the NW highlands, South Africa (red squares), showing dense, large pits on the disc and scattered pits on the elytra; Tanzania, Mozambique records of *S. interstitialis* require validation.

Locality data (mean ± SD, range): NE lowlands: Altitude: 301 ± 239, 0–1 000 m; annual rainfall: 672 ± 159, 383–971 mm; annual temperature (max. + min. /2): 22.5 ± 1.2, 20.9–25.2°C (N=20) (black squares). NW uplands: Altitude: 1 151 ± 315, 323–1 510 m; annual rainfall: 584 ± 93, 403–765 mm; annual temperature (max. + min. /2): 18.8 ± 1.9, 16.2–23.0°C (N=20) (red squares).

Habitat: No quantitative assessment; '*S. ebenus*' recorded from deep sand in open woodland, *S. interstitialis* from sandy loam in grassland and open woodland.

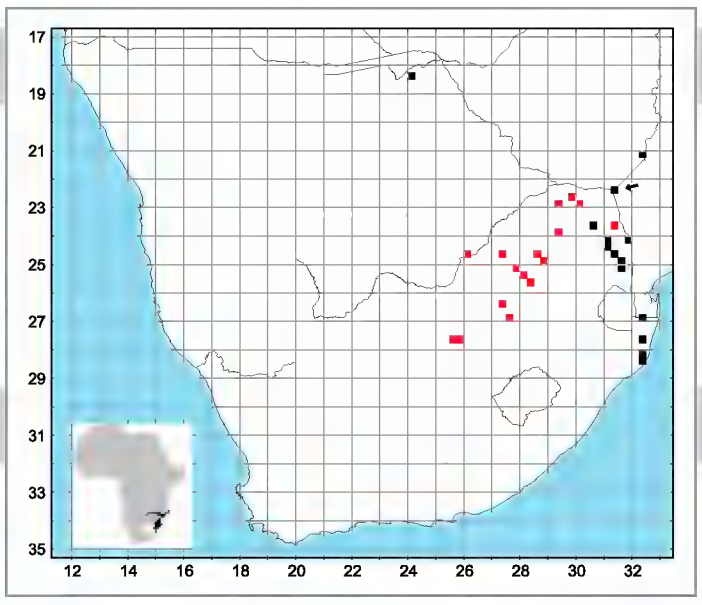
Food types: No quantitative assessment; '*S. ebenus*' sampled to omnivore dung (pig) at Phalaborwa (4) and Chobe National Park (3).

Temporal activity: Diurnal flight activity in the summer rainy season (Nov. to Feb.).

Ecoregions Botswana, Zimbabwe: *S. ebenus*: Zambezian and Mopane Woodlands (AT0725).

Bioregions South Africa: '*S. ebenus*': centred on Lowveld (SVl) (Savanna Biome); *S. interstitialis*: centred on Central Bushveld (SVcb) (Savanna Biome), N Dry Highveld Grassland (Gh) (Grassland biome).

Assessment rationale: EOO = 119 975 km² (*S. interstitialis*: NW uplands, white), EOO = 422 685 km² (*S. ebenus*: NE lowlands, black); identity and distribution uncertain; possible associations of '*S. ebenus*'



S. ebenus

S. interstitialis

Scarabaeus ebenus & *S. interstitialis* (continued)

with E coastal sands and '*S. interstitialis*' with sandy loam, but quantitative support required; probably no serious threats despite apparent low population density over much of their ranges; however, taxonomic uncertainty (one or two species) and poor support for ecological differences demands an assessment as Data Deficient (DD).

Conservation measures: Taxonomic revision is required before conservation status can be assessed; quantitative data on ecological associations is also required; in South Africa, protected in Kruger National Park ('*S. ebenus*'), Abe Bailey, Borakalalo and Tswaing nature reserves ('*S. interstitialis*').

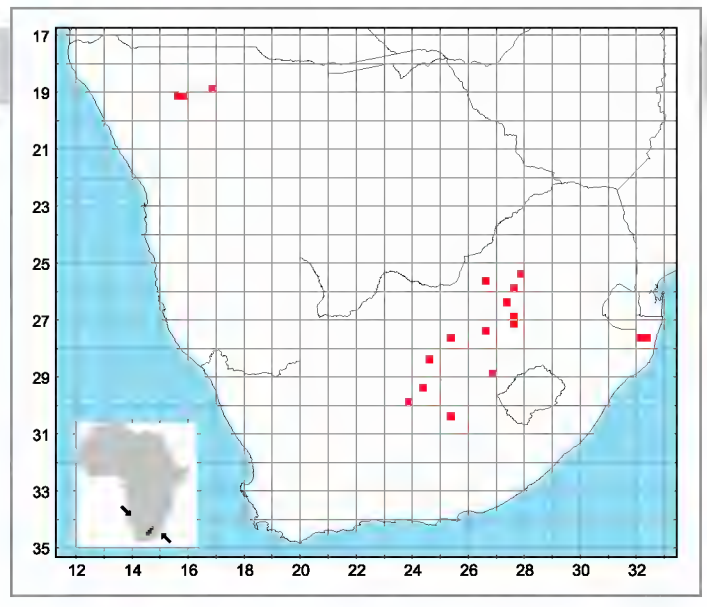
Scarabaeus funebris

(Boheman, 1857)

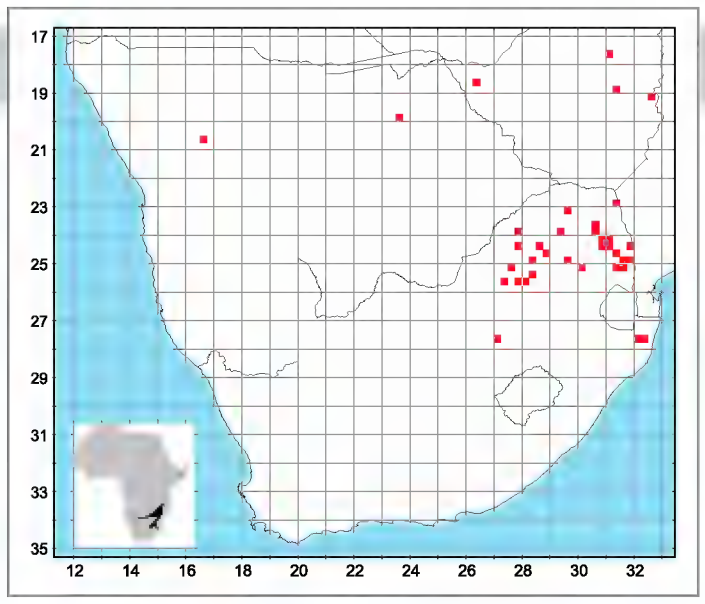
= *Scarabaeus funebris pretoriensis* Janssens, 1940b

Global: DD
Endemic: RSA, Namibia

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: As *Ateuchus funebris*: 'Caffraria interiore' [interior of SE South Africa]; *S. funebris pretoriensis*: Not explicitly stated.
Taxonomy: Accepted species.
Distribution: Validated records from one coastal and two upland centres: coastal KwaZulu-Natal and drier W Highveld, South Africa, N plateau, Namibia; also reported from Zimbabwe, Botswana.
Locality data (mean ± SD, range): Altitude: 1 135 ± 444, 55–1 559 m; annual rainfall: 538 ± 146, 304–743 mm; annual temperature (max. + min. /2): 18.9 ± 2.6, 15.5–23.0°C (N=22).
Habitat: No quantitative assessment; DBRU records mainly from finer-grained soils: sand (2), sandy loam (5), sandy clay loam (6) in grassland (3), scrub/shrubland (3), open woodland (7).
Food types: No quantitative assessment; DBRU records from dung of cattle (6), wildebeest (1), elephant (1), zebra (3), springbok (1).
Temporal activity: Diurnal flight activity during the summer and late summer rainy seasons (Oct. to Apr.).
Ecoregions Namibia: Angolan Mopane Woodlands (AT0702).
Bioregions South Africa: Dry Highveld Grassland (Gh) (Grassland Biome); NE Upper Karoo (NKu) (Nama Karoo Biome); E Eastern Kalahari Bushveld (SVk), S Central Bushveld (SVcb), S Lowveld (SVl) (Savanna Biome).
Assessment rationale: EOO = 104 390 km^2; wide range, but infrequently recorded; biogeographically and ecologically poorly known; AOO might be limited by soil type association; most DBRU collection records (63%, n=10/16) are from two game reserves; assessed as Data Deficient (DD).
Conservation measures: A quantitative survey needs to determine if the AOO is truly disjunct as is likely, or, merely a collection artefact; the ecological associations also need to be quantified; the frequency of game reserve records may be related to association with pellet-dropping herbivores and this needs to be tested; protected in uMkhuze Game Reserve, Abe Bailey Nature Reserve (South Africa), Etosha National Park (Namibia).



Scarabaeus galenus

Westwood, 1847

= *Ateuchus paradoxus* Boheman, 1857
= *Sebasteos adelphus* Kolbe, 1895

Global: LC (see IUCN Red List – LC)*

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Scarabaeus* (*Sebasteos*) *galenus*: 'Africa meridionali.....in the hilly country lying between 25° and 26° south lat. and 27° and 28° east long.' [Gauteng region, South Africa]; *A. paradoxus*: 'prope fluvium Limpopo' [near River Limpopo, southern Africa]; *S. adelphus*: 'Mkatta fluss in Usagara' [Mkatta River, Tanzania].

Taxonomy: Accepted species.

Distribution: Widespread in mostly drier, lower-altitude, sandy savannas of SE and S Central Africa: South Africa, N Namibia, N Botswana, Zimbabwe, Tanzania; also reported from Zambia.

Locality data (mean ± SD, range): Altitude: 750 ± 438, 55–1 495 m; annual rainfall: 630 ± 90, 436–850 mm; annual temperature (max. + min. /2): 20.6 ± 1.7, 16.9–23.6°C (N=43).

Habitat: No quantitative assessment; DBRU collection records biased to sandier soils: sand (6), sandy loam (5), sandy clay loam (1), and partially shaded vegetation: grassland (2), open woodland (9).

Food types: At Phalaborwa: strong bias to dung of ruminant herbivores (cattle: 21) rather than monogastric herbivores (elephant: 1) and omnivores (pig: 4); supported by DBRU collection records from cattle (8), wildebeest (1), buck (1), rhinoceros (2); but, prominence of two central clypeal teeth and observations of association with impala middens may indicate ready use of dung dropped as pellets.

Temporal activity: Diurnal flight activity during the summer rainy season (Oct. to Apr.); at Phalaborwa: primarily active on a warm day soon after heavy rainfall (24) than on a hot dry (1) or warm cloudy day (1) after light rainfall.

Ecoregions Namibia, Botswana, Zimbabwe: Angolan Mopane Woodlands (AT0702), Zambezian and Mopane Woodlands (AT0725), Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 699 090 km^2; AOO would likely be smaller owing to bias to woody vegetation on sandy soils although quantitative support is required; widely recorded in both farmland and reserves although clearance of woodland would probably be detrimental to population density; in South Africa, transformation 0–58% (SVl), 2–49% (SVcb), 0–20% (SVmp); assessed as Least Concern (LC) on basis of wide range. *IUCN Red List for *S. galenus* also includes data for *S. vicinus* Janssens, 1940b.

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, particularly relative bias to woodland on sandy soils and relative use of antelope pellets compared to other dung types; protected in Kruger National Park (South Africa).

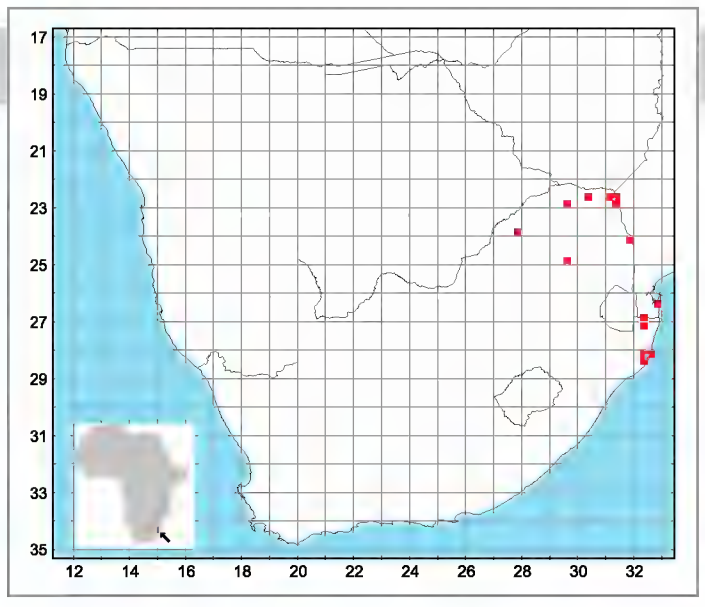
Scarabaeus geminogalenus

Davis & Deschodt, 2017

= *Sebasteos westwoodi* (Harold, 1869a) *sensu* Péringuey, 1908

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: *S. geminogalenus*: 'ST. LUCIA ESTUARY, Natal.' [KwaZulu-Natal, South Africa]; *S. westwoodi sensu* Péringuey: cited from 'Transvaal (Soutpansberg)' [Limpopo Province, South Africa].

Taxonomy: Accepted species; recently re-described as new after misidentification as *Scarabaeus westwoodi* Harold, 1869a, and synonymy with *S. galenus* Westwood, 1847.

Distribution: Primarily Limpopo River Valley and coastal deep sands: SE Mozambique, NE KwaZulu-Natal in South Africa.

Locality data (mean ± SD, range): Altitude: 380 ± 416, 0–1 331 m; annual rainfall: 652 ± 176, 455–971 mm; annual temperature (max. + min. /2): 21.8 ± 1.6, 17.1–23.4°C (N=16).

Habitat: No quantitative assessment of soil type, but many records from sand patches or areas of deep sands; on deep sands in Maputo Elephant Reserve: mostly in grassland (15) as opposed to dune forest (1); supported by DBRU collection records in grassland (4) and thicket (1).

Food types: No quantitative assessment; DBRU collection records from dung of cattle (1), rhinoceros (1).

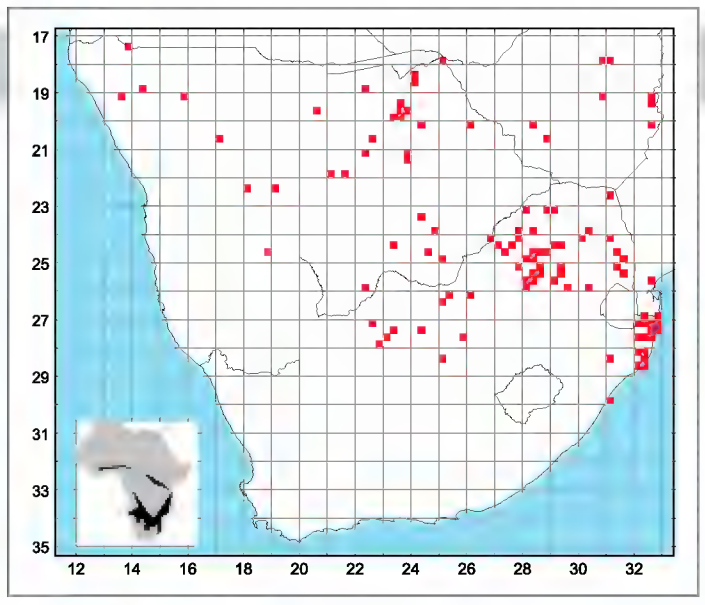
Temporal activity: Diurnal flight activity with long seasonal activity due to occurrence in the warm coastal lowlands (Aug. to May).

Ecoregions Mozambique: Maputaland Coastal Forest Mosaic (AT0119).

Bioregions South Africa: Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome); N Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 40 770 km^2; limited data suggest the AOO would be much smaller, centred in open vegetation on deep sand although quantitative support for soil associations is lacking; currently assessed as Least Concern (LC) on the basis of fairly wide range in open vegetation at a number of locations, of which the E records are entirely within reserves.

Conservation measures: Further quantitative data on ecological associations is required to support the assessment of conservation status, particularly soil and food association data; protected in Kruger National Park, iSimangaliso Wetland Park (World Heritage Site) (South Africa), Maputo Special Reserve (Mozambique).



Scarabaeus goryi

(Castelnau, 1840)

= *Ateuchus profanus* Boheman, 1857
= *Scarabaeus nepos* Fairmaire, 1884b
= *Scarabaeus sacer* var. *laevigatus* Kolbe, 1887
= *Scarabaeus pacatus* Péringuey, 1901

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Ateuchus goryi*: 'Sénégal'; *A. profanus*: 'Portum Natalense' [Durban, South Africa]; *S. nepos*: 'Zanzibar'; *S. sacer* var. *laevigatus*: 'Chinchoxo' [Angola]; *S. pacatus*: 'Southern Rhodesia' [Zimbabwe].

Taxonomy: Accepted species; a very close Palaearctic/Oriental relative is classified under *Scarabaeus s. str.*

Distribution: Widespread in sandy, moist, open savanna regions from S, E and W Africa: Senegal, Côte d'Ivoire, Nigeria, Democratic Republic of the Congo (DRC), Kenya, Tanzania, Angola, Zimbabwe, Namibia, Botswana, Mozambique, South Africa; also reported from Gambia, Guinea, Togo, Gabon, Uganda, Malawi; Sudan and Somalia records may be *Scarabaeus isidis* (Castelnau, 1840), a close, arid-region relative.

Locality data (mean ± SD, range): Altitude: 807 ± 480, 0–1 503 m; annual rainfall: 593 ± 191, 171–1 010 mm; annual temperature (max. + min. /2): 20.5 ± 1.7, 15.6–23.4°C (N=136).

Habitat: In open woodland at Leeuwfontein Nature Reserve: strong bias to sand (43) rather than sandy loam (11) or stony sandy loam (4); on deep sand in Maputo Special Reserve: abundant in both grassland (27) and sand forest patches (small: 29, medium: 59, large: 40); DBRU collection records also indicate a deep sand specialist and vegetation generalist: sand (21), sandy loam (2) in grassland (13), shrubland (4), open woodland (7), forest (3).

Food types: In Botswana: bias to omnivore (pig: 14) rather than herbivore dung (cattle: 5, sheep: 1, elephant: 1); DBRU collection records reflect commonly sampled dung types: human/cattle mixture (2), cattle (21), wildebeest (1), warthog (1).

Temporal activity: Flight activity in darkness primarily during the summer rainy season (Oct. to May); also Aug. at the warmer coastline; attracted to light.

Ecoregions Namibia, Botswana, Zimbabwe, Mozambique: Deep sands: Namibian Savanna Woodlands (AT1316), Kalahari Xeric Savanna (1 309), Angolan Mopane Woodlands (AT0702), Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian and Mopane Woodlands (AT0725), Southern Miombo Woodlands (AT0719), Southern African Bushveld (AT0717), Maputaland Coastal Forest Mosaic (AT0119).

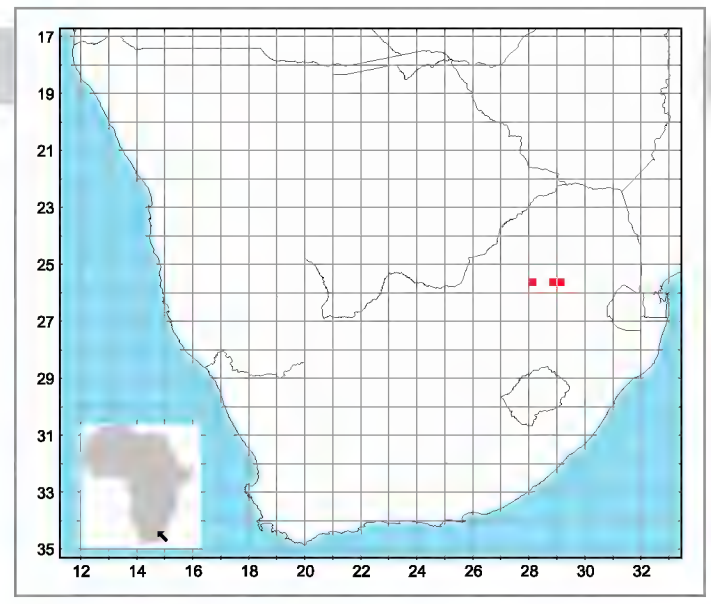
Bioregions South Africa: Centred on Eastern Kalahari Bushveld (SVk), Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome), Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 2 990 240 km^2; AOO rather more restricted due to specialisation to deep sands, but still widespread in open or shaded vegetation from drier SW Africa to moist tropical savanna where it may show a bias to omnivore dung although it is also readily attracted to the dung of domestic livestock; assessed as Least Concern (LC).

Conservation measures: None recommended; protected in various reserves including Tembe Elephant Park (South Africa), Bicuar National Park (Angola).

Scarabaeus heqvisti

zur Strassen, 1962

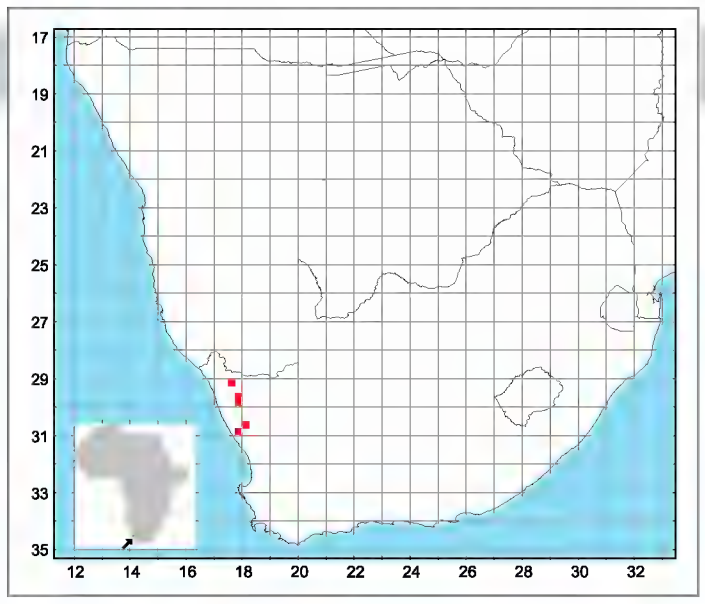


No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Magalies-berge, Transvaal' [South Africa].
Taxonomy: Accepted species.
Distribution: To date, recorded only along the E–W trending Magaliesberg range at the N edge of the South African Highveld on the transition between grassland and bushveld.
Locality data (mean ± SD, range): Altitude: 1 173 ± 202, 1 043–1 405 m; annual rainfall: 652 ± 42, 625–701 mm; annual temperature (max. + min. /2): 18.8 ± 1.0, 17.6–19.4°C (N=3).
Habitat: No adequate quantitative assessment; in Ezemvelo (now Telperion) Nature Reserve, Gauteng: recorded mainly in upland grassland on a patch of very sandy soils (1 419 m); rare in grassland on sandy soils at 1 338 m; not recorded on sandy loam or in open woodland on koppies.
Food types: No quantitative assessment; sampled to composite baits of pig and cattle dung.
Temporal activity: Diurnal flight activity in the summer rainy season (Oct. to May); absence in mid-summer undoubtedly a collecting artefact.
Bioregions South Africa: Vegetation unit: Rand Highveld Grassland (Gm 11) (Mesic Highveld Grassland (Gm), Grassland Biome); Vegetation unit: Moot Plains Bushveld (SVcb 8) (Central Bushveld (SVcb), Savanna Biome).
Assessment rationale: EOO = 305 km^2; although under protection in at least one reserve where it may show highly localised abundance after rainfall, the extremely small known EOO in few locations on a single mountain system would qualify this species for a IUCN threat category of at least Near Threatened (NT) or Vulnerable (VU), particularly as it is centred in an area where vegetation units are 28–50% transformed by cultivation, urbanisation or mining; as the full EOO and AOO are currently unknown, assessed as Data Deficient (DD).
Conservation measures: To assess the conservation status of this species, a quantitative survey is required to determine its full EOO and the ecological associations that restrict its AOO; the survey should focus on patches of sandy and other soil types in the Magaliesberg and nearby mountain blocks, and also determine possible effects of pasture modification; currently protected in Telperion Nature Reserve where it is, nevertheless, abundant on sandy soils after rainfall.



Scarabaeus hottentorum

Péringuey, 1901

= *Sebasteos procles* Kolbe, 1908

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *S. hottentorum*: 'Cape Colony (Namaqualand, Barkly West)' [South Africa]; *S. procles*: 'Klein-Namaland' [Namaqualand].

Taxonomy: Accepted species; of the type localities: Namaqualand in NW South Africa is considered correct, Barkly West in central South Africa is considered an error; classified in the genus, *Ateuchetus* Bedel, 1892, in the 2019 version of Catalogue of Life.

Distribution: Namaqualand, South Africa; recorded along the upper edge of the W escarpment in the N as well as coastal regions in the S.

Locality data (mean ± SD, range): Altitude: 564 ± 323, 99–1 116 m; annual rainfall: 126 ± 21, 93–154 mm; annual temperature (max. + min. /2): 17.6 ± 0.7, 16.2–18.3°C (N=7).

Habitat: No quantitative assessment; limited DBRU collection records from sand (1), sandy loam (1) in scrub/succulent Karoo (2).

Food types: No quantitative assessment; limited DBRU collection records from human (1) and cattle dung (1).

Temporal activity: Diurnal flight activity recorded in spring (Aug., Sept.) towards the end of the winter rainy season.

Bioregions South Africa: Centred on Namaqualand Hardeveld (SKn) (Succulent Karoo Biome).

Assessment rationale: EOO = 3 335 km^2; qualifies for an IUCN threat category of at least Vulnerable (VU) on the basis of small range (< 5 000 km^2) and few recorded localities; however, its arid EOO probably largely equates to its AOO, which is little transformed (0–6%) as it is used primarily for grazing of farm livestock; the effects of transformation for cultivation of winter wheat are unclear; currently poorly known and assessed as Data Deficient (DD).

Conservation measures: Before conservation status may be assessed, a quantitative survey is required to better determine the EOO, AOO and ecological associations; not currently known from any reserves, but probably not threatened owing to limited regional transformation.

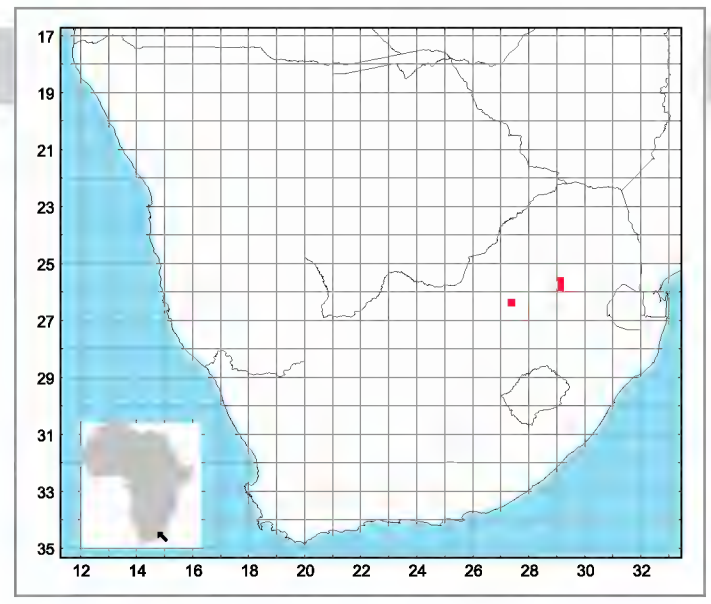
Scarabaeus karae

Davis & Deschodt, 2017

No synonyms (but see Taxonomy)

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: 'Abe Bailey NR, Gauteng, S26°17'–21' E027°16'–18', 1 496 m–1 544 m' [South Africa].

Taxonomy: Accepted species; newly described, smaller-bodied, close relative of *Scarabaeus funebris* (Boheman, 1857); aedeagus quite different; further new species, *Scarabaeolus orientalis* (Zídek & Pokorný, 2018), is considered an unpublished synonym of *Scarabaeus karae* (see Preamble).

Distribution: Known from a few points at the type locality (Abe Bailey Nature Reserve) and recently recorded as a rarity at two other localities, respectively, on a farm and near a rehabilitating mined area along the N edge of the Highveld, South Africa.

Locality data (mean ± SD, range): Altitude: 1 447 ± 110, 1 284–1 521 m; annual rainfall: 676 ± 20, 661–705 mm; annual temperature (max. + min. /2): 16.9 ± 0.8, 16.0–17.8°C (N=4).

Habitat: No quantitative assessment; sampled on sandy loam in natural grassland (Abe Bailey) or on sand, either in degraded natural grassland (farm) or a natural grassland patch surrounded by areas of mining and rehabilitation.

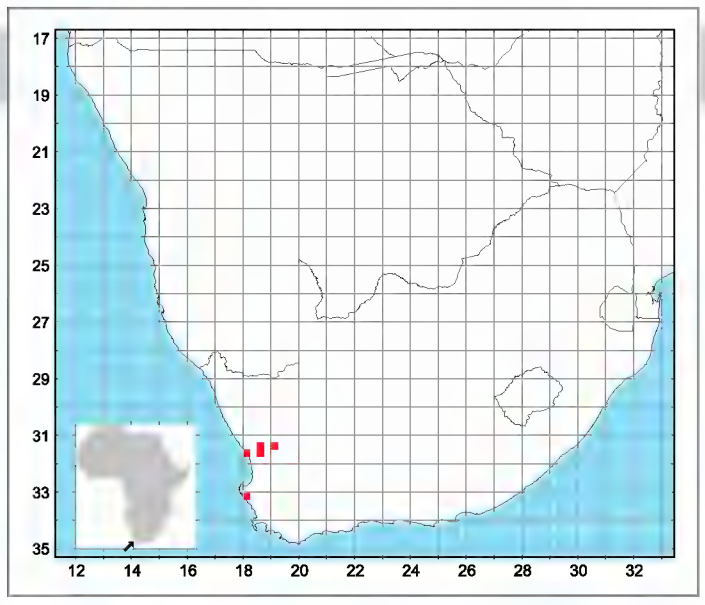
Food types: No quantitative assessment; sampled to composite baits of pig and cattle dung.

Temporal activity: Diel flight periodicity unknown, but presumably diurnal based on black pilosity; recorded in the summer rainy season (Dec., Mar.).

Bioregions South Africa: Vegetation units: Carletonville Dolomite Grassland (Gh 15) (Dry Highveld Grassland (Gh)); N edge of Eastern Highveld Grassland (Gm 12) (Mesic Highveld Grasslnd (Gm)) (Grassland Biome).

Assessment rationale: EOO = 3 080 km^2 (presumably underestimated); only known from natural grassland on sand and sandy loam in vegetation units that are 25–44% transformed by cultivation, urbanisation or mining; otherwise ecologically poorly known; *S. karae* would qualify for an IUCN threat category of at least Endangered (EN) on the basis of records from < 5 locations within an EOO < 5 000 km^2; however, the EOO is presumably underestimated and a collection artefact; therefore, *S. karae* is currently assessed as Data Deficient (DD).

Conservation measures: To assess conservation status, a quantitative survey is required in drier grasslands of the NW Highveld; this needs to determine the full EOO, AOO and ecological associations, particularly if habitat transformation is a detrimental influence on the AOO (mining, cultivation and pasture improvement); protected in Abe Bailey Nature Reserve (South Africa).



Scarabaeus piliventris

zur Strassen, 1962

No synonyms

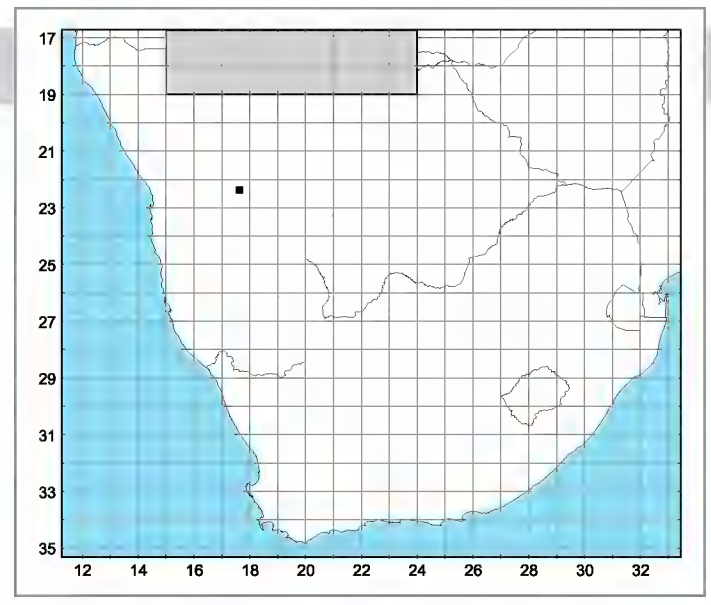
Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Saldanha Bay, Hopefield Distrikt' [Western Cape, South Africa].
Taxonomy: Accepted species.
Distribution: SW coastal lowlands and upper edge of SW escarpment, Western Cape, South Africa.
Locality data (mean ± SD, range): Altitude: 295 ± 299, 2–705 m; annual rainfall: 181 ± 44, 145–269 mm; annual temperature (max. + min. /2): 17.8 ± 1.3, 15.5–19.2°C (N=6).
Habitat: No quantitative assessment; one DBRU collection record from sandy loam in 'herbaceous pasture' cleared of natural shrubland; also recorded in coastal bioregions characterised by deep sands.
Food types: No quantitative assessment; one DBRU collection record from cattle dung.
Temporal activity: Diurnal flight activity recorded in late winter (July) and spring (Sept.) towards the end of the winter rainy season.
Bioregions South Africa: Primarily bioregions either side of the transition between the Fynbos (F) and Succulent Karoo Biomes (SK): Western Strandveld (F 11), Northwest Fynbos (FO 1), Namaqualand Sandveld (SKs), Knersvlakte (SKk), W Trans-Escarpment Succulent Karoo (SKt).
Assessment rationale: EOO = 3 305 km^2; the small known range and low number of localities in an area subject to 10–70% transformation by cultivation, urbanisation and mining would qualify this species for an IUCN threat category of at least Vulnerable (VU); however, represented by relatively few museum specimens and poorly known; assessed as Data Deficient (DD).
Conservation measures: A quantitative survey is required to determine the full EOO, AOO and ecological associations before an assessment may be made of conservation status; the effect of habitat transformation needs to be studied as one of six known localities (Nieuwoudtville) was in an area widely transformed into pasture; not currently known from any reserve.

Scarabaeus plausibilis

Péringuey, 1892



No synonyms

Global: DD

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: Not stated.

Taxonomy: Accepted species, but status requires validation in comparison to close, previously described relatives, namely: *Scarabaeus sulcipennis* (Quedenfeldt, 1888) and *Scarabaeus poggei* (Waterhouse, 1890), both cited from inexact type localities in S Democratic Republic of the Congo (DRC).

Distribution: *S. plausibilis* cited from Angola plus Ovamboland in Namibia; overlapping citations for *S. poggei* (Katanga in Democratic Republic of the Congo (DRC), Lunda in Angola) and *S. sulcipennis* (Kassai in Democratic Republic of the Congo (DRC), Lunda in Angola, Namibia).

Locality data: No precise data on map other than a suspect locality '30 m W of Windhoek' [central Namibian uplands] (black square); grey shaded panel estimates S edge of EOO with respect to citation from Ovamboland, inexact locality along 'Okavango R', and record from Liuwa Plains, SW Zambia (S14.6433 E22.6264) (to N of E end of grey panel).

Habitat: No quantitative assessment; citation from Ovamboland and records from Okavango River and Liuwa Plains may indicate an association with deep sands on floodplain grassland.

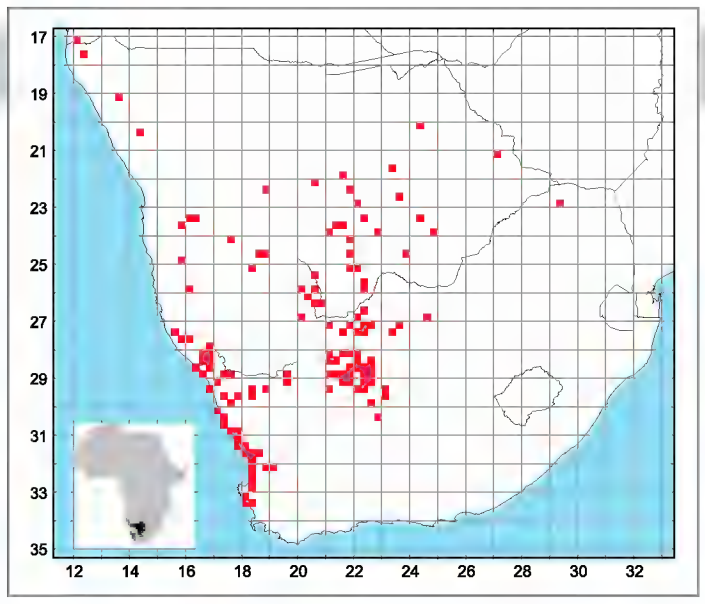
Food types: No quantitative assessment; sampled to pig dung.

Temporal activity: Diel flight periodicity unknown, but probably diurnal based on black pilosity; recorded during the summer rainy season (Nov.).

Ecoregions Zambia: A single exact record on Liuwa Plains: Western Zambezian Grasslands (AT0724).

Assessment rationale: EOO unclear but at least from Ovamboland to Liuwa Plains (grey panel); AOO would be much smaller if specialised to moist flood plain grasslands; assessed as Data Deficient (DD) owing to taxonomic uncertainty and poor ecological knowledge.

Conservation measures: A survey of N Namibia, E Angola, S Democratic Republic of the Congo (DRC) and SW Zambia is required to obtain further material and resolve questions on validity of nomenclature: how many species, three, two or only one; survey should determine the full EOO, AOO and provide quantitative data on ecological associations; no current records known from reserves.



Scarabaeus proboscideus

(Guérin-Meneville, 1844)

= *Ateuchus modestus* Boheman, 1860
= *Scarabaeus rostratus* Péringuey, 1888

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Ateuchus proboscideus*: 'le Cap de Bonne-Espérance' [Cape of Good Hope, South Africa]; *A. modestus*: 'prope lacum Ngami' [near Lake Ngami, Botswana]; *S. rostratus*: 'Spektakel, Namaqualand... Kenhardt and Bushmanland' [Northern Cape, South Africa].

Taxonomy: Accepted species; one of two species, until recently, included in the genus *Neateuchus* Gillet, 1911.

Distribution: Widespread on deep sands from the arid SW Kalahari to the SW coast and N along inland edge of Namib Desert to the Kaokoveld; South Africa, Botswana, Namibia, Angola.

Locality data (mean ± SD, range): Altitude: 808 ± 424, 0–1 782 m; annual rainfall: 219 ± 95, 29–525 mm; annual temperature (max. + min. /2): 18.8 ± 1.6, 14.5–22.3°C (N=222).

Habitat: No adequate quantitative assessment; in Northern Cape: recorded primarily in Kalahari (n=91 sites) and N Bushmanland (n=23); in Western Cape: sampled primarily from shrubland on deep sand (Modderrivier: 10, Pampoenvlei sand: 52, Pampoenvlei sandy loam: 2); DBRU collection records exclusively from deep sands (14) in open woodland, shrubland or grassland (3), scrub (3), shrubland (7), open woodland (1).

Food types: On deep sands in Botswana: most strongly attracted to dung of pellet-dropping sheep (1 182), also sampled in abundance to other dung types: pig (252), elephant (112), cattle (163), rare on carrion (chicken livers: 1); DBRU collection records from dung of cattle (11) and donkey (1).

Temporal activity: Flight activity in darkness; observed flying up to 23:00 in the Kalahari at 26°C; attracted to light; in SW winter rainfall region: active in warmer, dry, early summer (Oct., Nov.) tailing off into mid-summer (Dec. to Feb.); in NE: primarily active during late summer rains.

Ecoregions Namibia, Botswana: Centred on deep sands of Succulent Karoo (AT1322), Namibian Savanna Woodlands (AT1316), Kalahari Xeric Savanna (AT1309), marginal occurrence in three adjoining ecoregions.

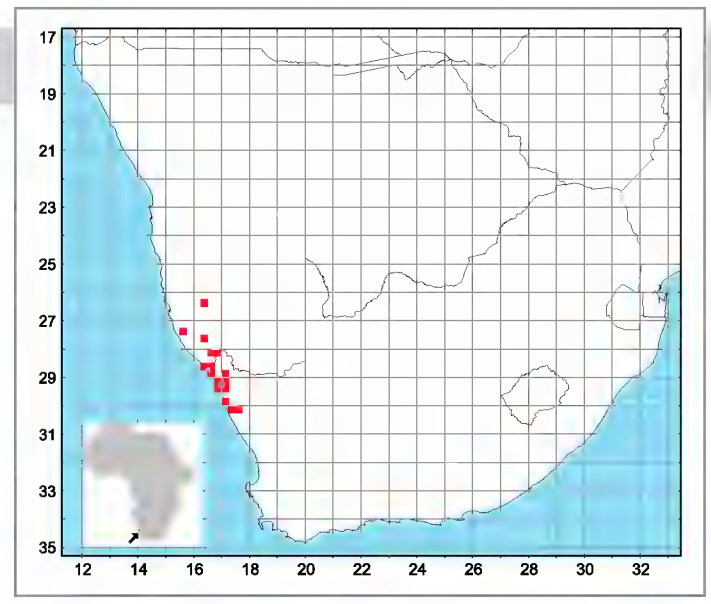
Bioregions South Africa: Centred on deep sands of Eastern Kalahari Bushveld (SVk), Kalahari Duneveld (SVkd), (Savanna Biome); N Bushmanland (NKb) (Nama Karoo Biome); Namaqualand Sandveld (SKs) (Succulent Karoo Biome); Western Strandveld (F 11) (Fynbos Biome).

Assessment rationale: EOO = 502 100 km^2; observed to be a sand specialist although poorly supported by available data; AOO would be similar to EOO owing to large extent of deep sands across its wide range that is little transformed and used primarily for the grazing of domestic livestock or conservation; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data to support observed specialisation to deep sands in open vegetation; protected in Central Kalahari Game Reserve (Botswana), Kgalagadi Transfrontier Park, coastal portion of Namaqua National Park (South Africa) and Sperrgebiet National Park (Namibia).

Scarabaeus proximus

Péringuey, 1901



No synonyms

Global: LC
Endemic: RSA, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Cape Colony (Namaqualand), Port Nolloth' [South Africa].

Taxonomy: Accepted species; one of three species, until recently, included in the genus *Drepanopodus* Janssens, 1940.

Distribution: Centred on arid sands to the S and N of the Orange River: South Africa, Namibia.

Locality data (mean ± SD, range): Altitude: 274 ± 243, 1–940 m; annual rainfall: 62 ± 22, 32–115 mm; annual temperature (max. + min. /2): 15.9 ± 0.8, 14.5–17.6°C (N=24).

Habitat: No quantitative assessment; all South African records (9) recorded from areas of deep sands in Succulent Karoo.

Food types: No quantitative assessment; sampled to pig dung.

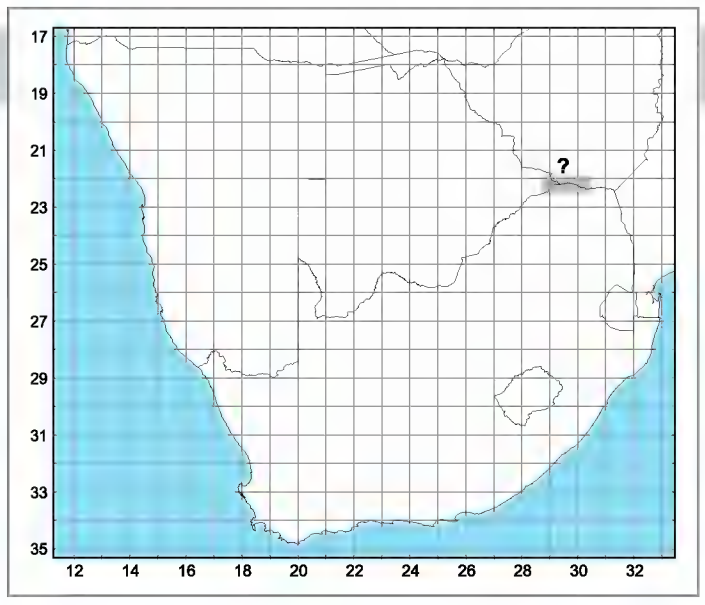
Temporal activity: Presumably diurnal flight activity on the basis of black pilosity; recorded in autumn (May) and from late winter to early summer (July to Dec.) at the end of the winter rainy season and early dry season.

Ecoregions Namibia: Primarily Succulent Karoo (AT1322), one record at extreme S margins of Namib Desert (AT1315).

Bioregions South Africa: Only in arid N Namaqualand Sandveld (SKs) (Succulent Karoo Biome).

Assessment rationale: EOO = 16 030 km^2; observed to be a soil specialist, therefore, AOO would be restricted to areas of arid deep sands that are extensive within its limited lowland EOO; little protection in South Africa although transformation of SKs is only 0–10% primarily by mining along the N coastline; however, as the 50% of the EOO that occurs in Namibia is officially conserved, *S. proximus* is assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; in South Africa, only the extreme S range limits are protected in Namaqua National Park; however, most of its range in Namibia is protected in Sperrgebiet National Park.



Scarabaeus rixosus

Péringuey, 1901

No synonyms

Global: DD (see IUCN Red List – DD)

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Southern Rhodesia (Middle Limpopo)' [Zimbabwe].

Taxonomy: Accepted species; known only by the type specimen recently rediscovered in the reference collection of the National Collection of Insects, South Africa (Deschodt et al. 2017); not previously marked as a type, but clearly different to any other southern African *Scarabaeus* spp.; identified as *S. rixosus* from original description, with monofid spur on mentum as the defining diagnostic character; one of two species, until recently, included in the genus *Neateuchus* Gillet, 1911.

Distribution: Essentially unknown; middle (cited type locality) to upper Limpopo Valley (etiquette label on putative type specimen in Péringuey's handwriting); cited from Zimbabwe along border with South Africa; unclear if it would occur in South Africa.

Locality data (range): Estimated approximations; altitude: 560–830 m; annual rainfall: 290–330 mm; annual temperature (max. + min. /2): 23.0–24.5°C.

Habitat: No quantitative assessment; unknown; middle Limpopo Valley is an isolated island of low rainfall with expanses of loam and loamy sands on Zimbabwean side of border; South African side of border more heterogeneous although small patches of deep sands occur; putative close relative, *S. proboscideus* Guérin-Meneville, 1844, is a sand specialist (relationship based on shared character of spur on mentum).

Food types: No quantitative assessment; unknown.

Temporal activity: Unknown.

Ecoregions Zimbabwe: Speculative; Limpopo Valley extension of Zambezian and Mopane Woodlands (AT0725).

Bioregions South Africa: Speculative; Mopane (SVmp) (Savanna Biome).

Assessment rationale: EOO and AOO unknown; no ecological data whatsoever; only known by the single type specimen described over a century ago and with no subsequent records; could be truly rare and endangered or a collection artefact; currently assessed as Data Deficient (DD).

Conservation measures: A quantitative survey is required to determine EOO, AOO and ecological associations before an assessment of conservation status may be made; this should be conducted across the range of habitats found from the middle to the upper Limpopo Valley, particularly loamy sands (Zimbabwe) and deep sand patches (South Africa); not known to be protected in any reserve.

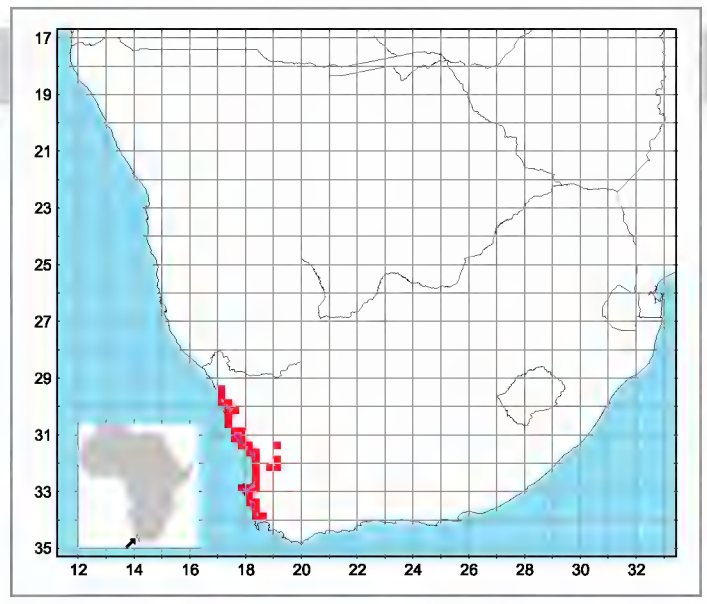
Scarabaeus rugosus

(Hausmann, 1807)

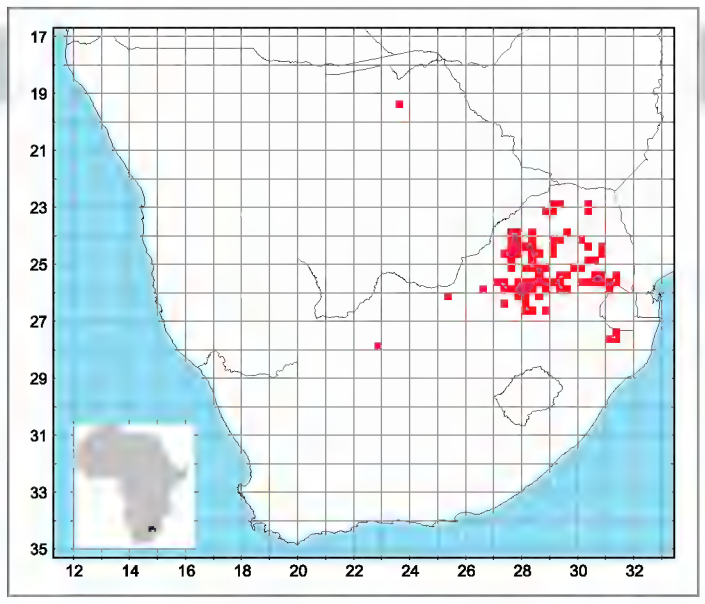
= *Ateuchus convalescens* Wiedemann, 1823

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: As *Ateuchus rugosus*: Not stated; *A. convalescens*: 'Prom. bon. sp.' [Cape of Good Hope, South Africa].
Taxonomy: Accepted species.
Distribution: Except for a few inland localities that require validation, restricted to dry west coastal sands in the winter rainfall region of South Africa.
Locality data (mean ± SD, range): Altitude: 98 ± 100, 0–636 m; annual rainfall: 186 ± 78, 48–393 mm; annual temperature (max. + min. /2): 17.2 ± 1.0, 15.2–18.7°C (N=86).
Habitat: In Western Cape: sampled primarily from shrubland on deep sand (Modderrivier: 307, Geelbek: 397, Pampoenvlei: 71); uncommon at adjacent sites: shrubland on sandy loam at Pampoenvlei (2), pasture created by clearance of shrubs on deep sand at Geelbek (12); DBRU collection records exclusively from deep sand (14) in scrub/shubland (9); single records in grassland and a fallow crop field.
Food types: No quantitative assessment; DBRU collection records from dung of cattle (15) and horse (1).
Temporal activity: Diurnal flight activity in sunshine, especially after rainfall as long as temperatures remain sufficiently high; on the SW coast: flight activity commences at about 21°C with a midday peak in the cooler early spring or a 09:00–10:00 peak in the warmer later spring; seasonal peaks of sclerotised adults in spring (July to Oct.) and both sclerotised and teneral adults in autumn (Mar. to May).
Bioregions South Africa: Centred on Namaqualand Sandveld (SKs) (Succulent Karoo Biome), West Strandveld (F 11) (Fynbos Biome); few localities in vegetation units of Sand Fynbos (FFd), (Northwest Fynbos (FO 1), Fynbos Biome).
Assessment rationale: EOO = 11 000 km^2; N part of range has been little transformed (3–10%); S part of range in Western Strandveld is from 25–50% transformed by cultivation and urban development; this would be detrimental considering the strong shrubland association; however, due to low transformation in the N and some protection in the S and N, currently assessed as Least Concern (LC).
Conservation measures: Assessment of conservation status would be improved by quantitative data on food associations; protected in the coastal portion of Namaqua National Park and in strandveld of West Coast National Park where patches of sparse grassland resulting from clearance of shrubs on the Farm Geelbek have now been replaced by regenerated shrubland.



Scarabaeus rusticus

(Boheman, 1857)

No synonyms

Global: LC
Endemic: RSA, Botswana, ?Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Ateuchus rusticus*: 'Caffraria tota' [inexact, may be interpreted as anything between all SE South Africa or all southern Africa].
Taxonomy: Accepted species.
Distribution: Drier upland grasslands and woodland patches on the N Highveld; also wooded rocky koppies in bushveld regions with a few outliers at the edge of the Kalahari; unclear if there is truly a disjunction between N Highveld and the Blouberg/Soutpansberg; mainly South Africa, marginal in Botswana; suspect outliers from uMkhuze Game Reserve (coastal KwaZulu-Natal) and Fish River Canyon (S Namibia) not included on map.
Locality data (mean ± SD, range): Average altitude: 1 228 ± 275, 563–2 005 m; average annual rainfall: 681 ± 122, 338–1 271 mm; average annual temperature (max. + min. /2): 18.3 ± 1.7, 12.5–22.4°C (N=156).
Habitat: No adequate quantitative assessment; in Telperion Nature Reserve: mainly on upland wooded koppies at 1 379–1 452 m (29.9 per sample), fewer in adjoining grassland at 1 419 m (12.0) or at distance from wooded areas in grassland at 1 338–1 389 m (1.1); limited DBRU collection records on sand (1), sandy loam (2), clay (1) in open woodland (4).
Food types: No quantitative assessment; limited DBRU collection records on dung of baboon (1), cattle (2).
Temporal activity: Diurnal flight activity primarily in the summer rainy season (Aug. to Apr.).
Ecoregions Botswana: Marginal in Zambezian and Mopane Woodlands (AT0725) (Okavango Swamps).
Bioregions South Africa: Centred on Central Bushveld (SVcb), also, E margin Lowveld (SVl) (Savanna Biome); N margin Mesic Highveld Grassland (Gm), N extremity Sub-Escarpment Grassland (Gs) (Grassland Biome); scattered records in two other bioregions.
Assessment rationale: EOO = 105 335 km^2 (main range in South Africa; does not include outliers); widespread in N South Africa where it is centred on drier, cooler upland areas in bushveld and at the edge of warmer N Highveld Grassland; AOO apparently centred on wooded patches in an often transformed region (SVcb: 1–49%), if so, clearance of trees would be detrimental to population density; however, locally abundant and found in various nature reserves; therefore, assessed as Least Concern (LC).
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, particularly, vegetation associations; protected in Telperion, Abe Bailey, Leeuwfontein nature reserves, also Ithala Game Reserve.

Scarabaeus savignyi

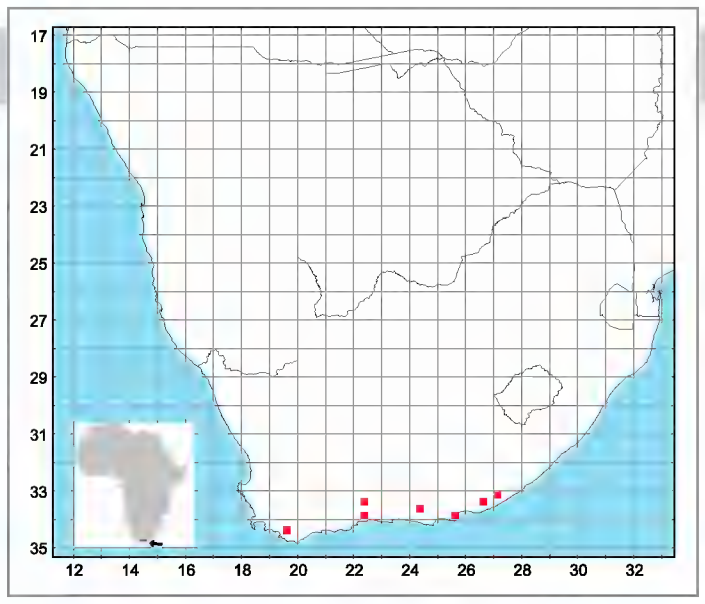
Macleay, 1821

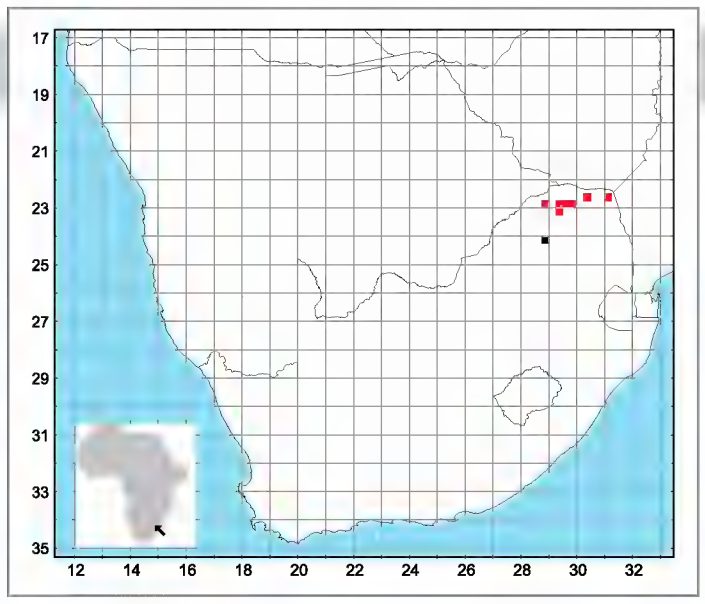
= *Ateuchus transversus* Castelnau, 1840

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Scarabaeus savignii*: Not stated; *A. transversus*: 'Cap de Bonne-Espérance' [Cape of Good Hope, South Africa].
Taxonomy: Accepted species; occurs in a phylogenetic clade together with Palaearctic species classified in the genus *Ateuchetus* Bedel, 1892; duly classified as an *Ateuchetus* species in the 2019 version of Catalogue of Life.
Distribution: S coastal lowlands, Western and Eastern Cape, South Africa; records from elsewhere in South Africa require validation; reports from Namibia, Zimbabwe, presumed as errors.
Locality data (mean ± SD, range): Altitude: 388 ± 264, 99–822 m; annual rainfall: 445 ± 112, 270–595 mm; annual temperature (max. + min. /2): 16.8 ± 1.0, 15.6–18.3°C (N=7).
Habitat: No quantitative assessment; two DBRU collection records from sandy clay loam, one from a fallow crop field.
Food types: No quantitative assessment; one DBRU collection record from cattle dung.
Temporal activity: Diurnal flight activity late in the Western Cape, winter rainy season (Oct.), or, the Eastern Cape, bimodal rainy season in spring / early summer (Oct. to Dec.) and autumn (Mar., Apr.).
Bioregions South Africa: Vegetation units: Sandstone Fynbos (FFs), Granite Fynbos (FFg), Limestone Renosterveld (FRl), Shale Renosterveld (FRs) (Fynbos Biome); Albany Thicket Biome (AT); Eastern Cape margin of Sub-Escarpment Savanna (SVs) (Savanna Biome).
Assessment rationale: EOO = 31 775 km^2; widespread along S coastal regions but very poorly known; AOO possibly influenced by finer-grained soils, but requires confirmation; natural shrubland vegetation widely transformed across range, but unclear if this influences current EOO and/or AOO; assessed as Data Deficient (DD).
Conservation measures: A quantitative survey of the full EOO, AOO and ecological associations is necessary before conservation status may be assessed; any possible effect of natural shrubland conversion to pasture grass should also be determined; protected in the Baviaanskloof Nature Reserve (Eastern Cape).





Scarabaeus schulzeae

Ferreira, 1969

No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'República da África do Sul – Transval: Great Saltpan' [salt-pan at W end of Soutpansberg, Limpopo Province, South Africa].
Taxonomy: Accepted species.
Distribution: Limpopo Province, South Africa; centred on and around the W–E trending Soutpansberg; one Waterberg locality requires validation (black square).
Locality data (mean ± SD, range): Altitude: 1 015 ± 326, 461–1 626 m; annual rainfall: 574 ± 99, 456–747 mm; annual temperature (max. + min. /2): 19.4 ± 2.1, 15.5–22.9°C (N=13).
Habitat: No quantitative assessment; a single DBRU collection record from sand in open woodland; one record from forest.
Food types: No quantitative assessment; a single DBRU collection record from cattle dung.
Temporal activity: Presumably diurnal flight activity on the basis of black pilosity; primarily active during the summer rainy season (Nov. to Mar.).
Bioregions South Africa: Vegetation units: Limpopo Sweet Bushveld (SVcb 19), Makhado Sweet Bushveld (SVcb 20), Soutpansberg Mountain Bushveld (SVcb 21), Musina Mopane Bushveld (SVmp 1), Makuleke Sandy Bushveld (SVl 1) (Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) in Savanna Biome).
Assessment rationale: Smaller EOO (red squares) = 2 500 km^2; larger EOO (includes Potgietersrus [Mokopane] locality, black square) = 5 500 km^2; very restricted, validated EOO would qualify *S. schulzae* for an IUCN threat category of at least Vulnerable (VU); AOO could be even more restricted if it shows specialised soil and vegetation type associations; range centred around SVcb 21 (21% transformed) in an area that is poorly conserved; currently not well known and assessed as Data Deficient (DD).
Conservation measures: A quantitative survey of EOO, AOO and ecological associations is required before conservation status may be assessed; one record from the N Kruger National Park (South Africa), but most of the range and most current records are from unprotected areas, including an area scheduled for mining.

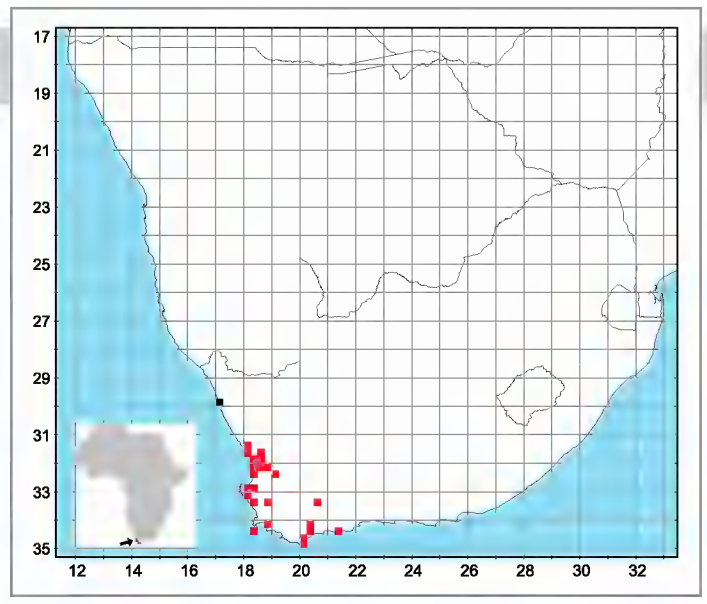
Scarabaeus suri

(Hausmann, 1807)

= *Ateuchus caffer*, Le Peletier & Serville, 1828
= *Scarabaeus hottentotus* Macleay, 1821

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: As *Ateuchus suri*: Not stated; *A. caffer*: 'Cap de Bonne-Espérance'; *S. hottentotus*: 'Cap. Bon. Spei.' [both Cape of Good Hope, South Africa].

Taxonomy: Accepted species.

Distribution: Primarily W and SW coastal regions, Western Cape Province, South Africa; outlier occurrence in Namaqualand (black square) requires validation.

Locality data (mean ± SD, range): Altitude: 214 ± 384, 0–1 924 m; annual rainfall: 276 ± 98, 99–466 mm; annual temperature (max. + min. /2): 16.7 ± 1.6, 8.7–18.9°C (N=38).

Habitat: No adequate quantitative assessment; in Western Cape: sampled in abundance from natural shrubland of cooler coastal deep sands (Cape of Good Hope Nature Reserve: open cover: 28, dense low cover of *Restio* spp.: 53, Modderrrivier: 31); rare in Kikuyu pasture (Bonne Attente: 1) adjoining Cape of Good Hope Nature Reserve, but super-abundant in dry sparse pasture grass on sandy loam in Darling Hills (Groote Post: 664); DBRU collection records biased to coarse-grained soils in open vegetation: sand (9), sandy loam (1), sandy clay loam (1) in pasture/grassland (5), scrub (3) and crop fields (2).

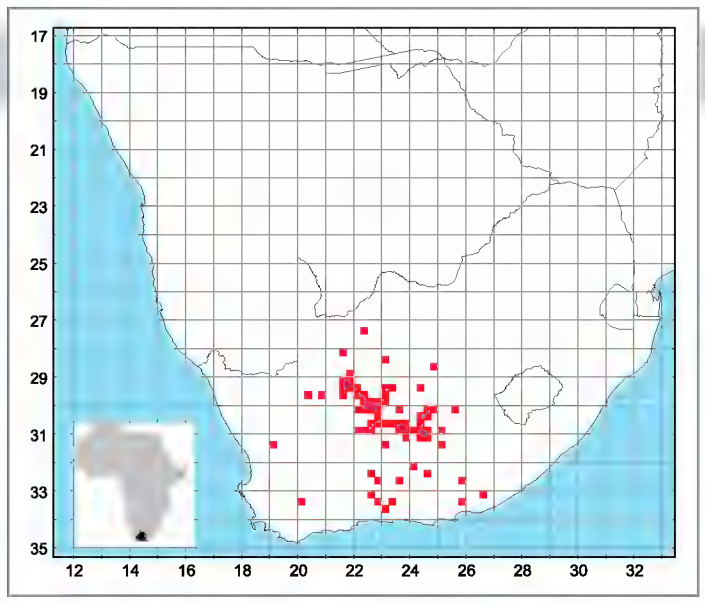
Food types: No quantitative assessment; DBRU collection records on dung: cattle (11), buffalo (1), horse (1).

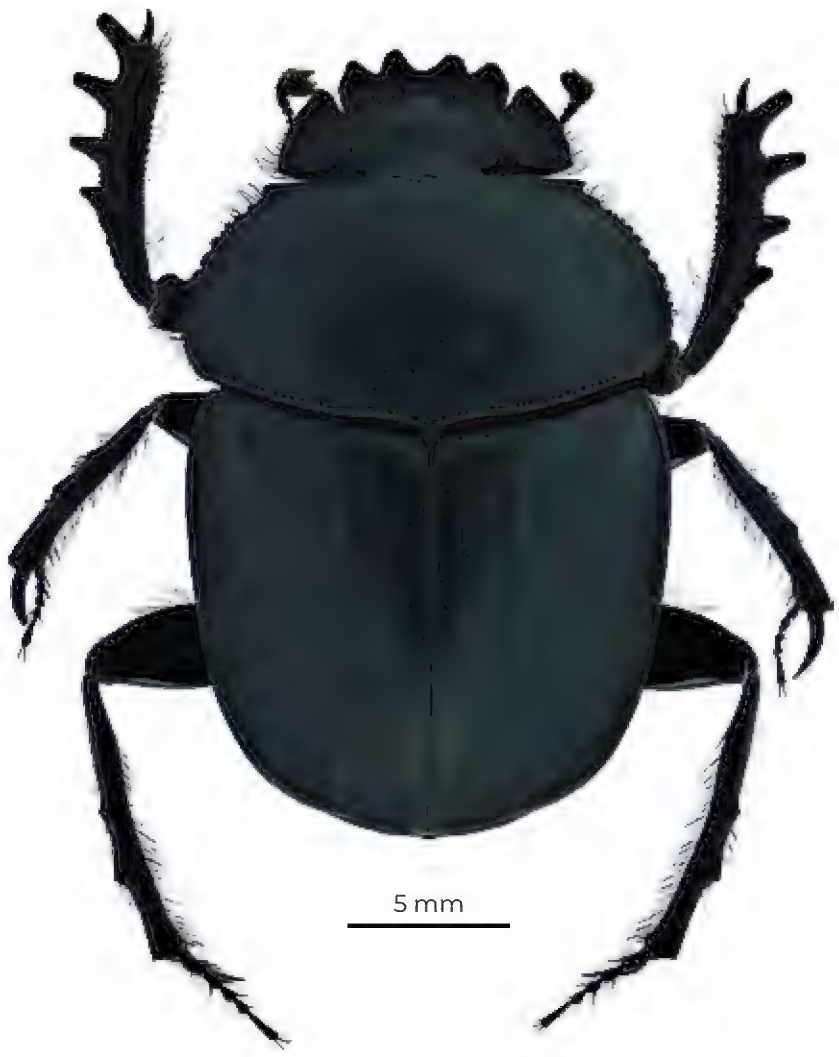
Temporal activity: Diurnal flight activity from late winter till following autumn (July to Apr.); primarily active in spring and summer (Sept. to Feb.); peak activity in early summer (Nov., Dec. – fully sclerotised) or mid- to late summer (Dec. to Feb. – tenerals).

Bioregions South Africa: Centred on SW vegetation units of Sand Fynbos (FFd), Sandstone Fynbos (FFs), Limestone Fynbos (FFl), Western Strandveld (F 11), Granite Renosterveld (FRg) (Fynbos Biome).

Assessment rationale: EOO = 23 250 km^2; widespread in open vegetation on sandy soils in drier parts of the Western Cape; highly transformed in many places (F 11: 25–70%; FFl: 14%; FRg: 80%; FFs: 15–75%; FFd: 40–80%); in Western Cape: results are conflicting with highest abundance in one pasture cleared of natural shrubs; otherwise primarily in natural shrubland vegetation on sand; currently assessed as Least Concern (LC) pending further study.

Conservation measures: Due to conflicting results, conservation status needs to be re-assessed after conducting a survey of association with soil type and natural shrubland versus transformed pasture habitats, including effects of surface cover density and irrigation; protected in Cape of Good Hope Nature Reserve (South Africa).





Scarabaeus viator

Péringuey, 1901

No synonyms

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'Rare in the western part of the Colony (Worcester, Beaufort West, Knysna), and more abundant in the eastern (Graham's Town, Port Elizabeth, Uitenhage)' [SW South Africa].

Taxonomy: Accepted species, but further work on Eastern Cape and Northern Cape populations would be useful to resolve past questions on their identity as *S. viator* or two different taxa.

Distribution: Arid SW South Africa; E range edge approaches that of the extremely closely related, *Scarabaeus ambiguus* (Boheman, 1857).

Locality data (mean ± SD, range): Altitude: 1 135 ± 223, 249–1 797 m; annual rainfall: 252 ± 63, 122–531 mm; annual temperature (max. + min. /2): 17.0 ± 1.7, 12.1–19.8°C (N=169).

Habitat: No adequate quantitative assessment; in the Northern Cape: present at almost every study site in floral regions of Upper Karoo (99.2% of sites, N=121) and an upland area to S of Orange River straddling the Upper Karoo/Bushmanland boundary (100%, N=68), rare in SW Kalahari (11.2%, N=98) and lower-lying areas of Bushmanland (3.0%, N=68); soil generalist in first two Northern Cape regions: sand (21.1/site), sandy loam (21.5), sandy clay loam (30.9); DBRU collection records on sand (4), sandy loam (6), sandy clay loam (4), clay (1) in grassland/pasture (3), scrub/shrubland (9).

Food types: No quantitative assessment; DBRU collection records on dung: cattle (11), buffalo (1), sheep (2), elephant (1), donkey (1).

Temporal activity: Diurnal flight activity during spring and summer across its range in winter, bimodal and late summer rainfall regions (Oct. to May).

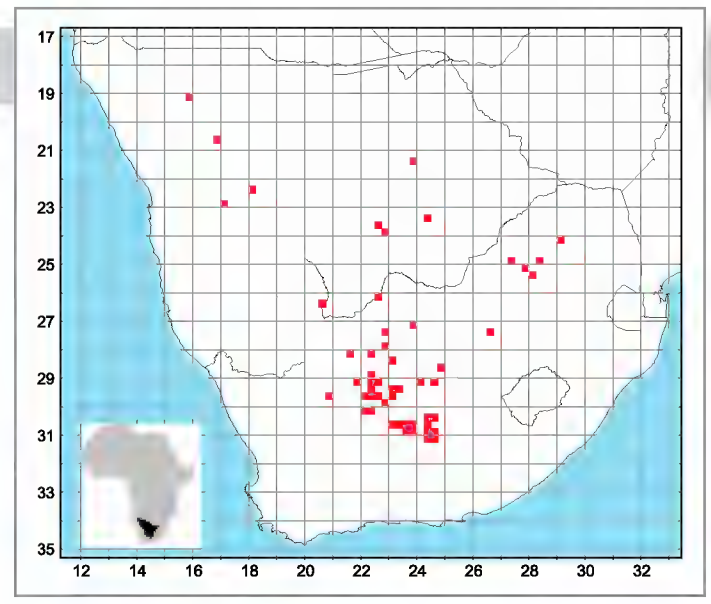
Bioregions South Africa: Upper Karoo (NKu), E Bushmanland (NKb), Lower Karoo (NKl) (Nama Karoo Biome); Albany Thicket Biome (AT); uncommon in Trans-Escarpment Succulent Karoo (SKt), Rainshadow Valley Karoo (SKv) (Succulent Karoo Biome); marginal NE records from two other bioregions/biomes.

Assessment rationale: EOO = 288 635 km^2; AOO would be about half of the EOO as *S. viator* is rare in the hot, extremely arid, low-altitude parts of Bushmanland lying between rare extreme SW records at the edge of the winter rainfall region and more frequent NE records in the higher altitude Upper Karoo; nevertheless, AOO is large in a little-transformed area where it is readily attracted to dung of farm livestock; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by balanced data on ecological associations; currently only known to be protected in Addo Elephant National Park (Eastern Cape, South Africa).

Scarabaeus vicinus

Janssens, 1940b

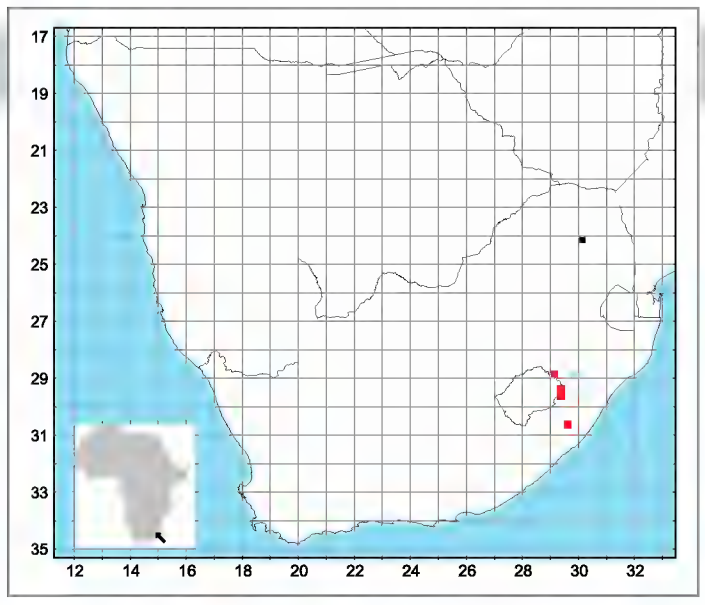


No synonyms

Global: LC
Endemic: RSA, Botswana, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Afrique australe intérieure' [interior, southern Africa].
Taxonomy: Accepted species; very close to *S. galenus* Westwood, 1847.
Distribution: Centred on drier areas: NE Nama Karoo, southern Kalahari; South Africa, Botswana, Namibia.
Locality data (mean ± SD, range): Altitude: 1 180 ± 205, 870–1 998 m; annual rainfall: 309 ± 117, 139–660 mm; annual temperature (max. + min. /2): 17.9 ± 2.0, 14.3–22.4°C (N=74).
Habitat: No adequate quantitative assessment; in Northern Cape survey: recorded at study sites on the continuous deep or loamy sands of SW Kalahari or sandy pans in the Upper Karoo and Karoo areas to S of Orange River (27), also sandy loam (21), but few on sandy clay loam (6); DBRU collection records primarily from sand (10), also sandy loam (2), sandy clay loam (1), in open vegetation that predominates in arid EOO, Grassland (5), scrub/shrubland (7), open woodland (1).
Food types: No quantitative assessment; DBRU collection records entirely from cattle dung (12).
Temporal activity: Diurnal flight activity recorded primarily in the late summer rainy season that predominates in the SW of the EOO (Oct. and Dec. to Mar.).
Ecoregions Namibia, Botswana: Kalahari Xeric Savanna (AT1309), margins of two adjoining ecoregions.
Bioregions South Africa: Bushmanland Nama Karoo (NKb), Upper Karoo (NKu) (Nama Karoo Biome); Eastern Kalahari Bushveld (SVk), Central Bushveld (SVcb) (Savanna Biome); marginal in two other bioregions.
Assessment rationale: EOO = 791 785 km^2; stronger supporting data is required to determine if AOO is limited by specialisation to coarser-grained soils, which are nevertheless widespread across the large EOO; may have been associated with dung of pellet-dropping mammals in past when large pads of ruminant herbivores were absent from SW part of range; now supported by farm livestock in a little-transformed area used primarily for grazing; assessed as Least Concern (LC).
Conservation measures: Assessment of conservation status would be improved by better quantitative data on ecological associations; protected in Central Kalahari Game Reserve (Botswana).



Scarabaeus westwoodi

Harold, 1869a

= *Scarabaeus laticeps* Péringuey, 1901

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *S. westwoodi*: 'Africa austr. inter.' [interior of southern Africa]; *S. laticeps*: 'Natal (Frere, Durban)' [KwaZulu-Natal, South Africa].

Taxonomy: Accepted species; synonymy of *S. laticeps* should be re-assessed owing to lower-altitude occurrence of type localities at Frere (blue square, 1 065 m) and Durban (inexact coastal locality) within the range occupied by a close relative, *S. caffer* (Boheman).

Distribution: Primarily known from high altitude natural grasslands on the Drakensberg escarpment along the E Lesotho border; wider distribution on the N escarpment edge (Mmafefe – black square) requires validation.

Locality data (mean ± SD, range): Altitude: 2 155 ± 695, 1 007–3 218 m; annual rainfall: 830 ± 85, 722–1 001 mm; annual temperature (max. + min. /2): 11.1 ± 4.0, 4.8–18.3°C (N=8). Frere: Average altitude: 1 065 m; average annual rainfall: 730 mm; average annual temperature (max. + min. /2): 17.2°C.

Habitat: No adequate quantitative assessment; across a gradsect up the Drakensberg escarpment: recorded in natural grassland on sandy clay loam at 1 900 m, 2 400 m and 2 800 m, but not at 1 500 m, 1 000 m or 500 m; but one DBRU collection record from sandy clay loam in pasture at ± 1 450 m (Gs 10 – see Bioregions).

Food types: No quantitative assessment; sampled to cattle dung; also one DBRU collection record from cattle dung; abundant at 1 900 m on the Sani Pass where no cattle were present.

Temporal activity: Diurnal flight activity (observed in Loteni Nature Reserve) during the summer rainy season (Nov. to Apr.).

Bioregions South Africa: Vegetation units: validated records on Sani Pass: Southern Drakensberg Highland Grassland (Gd 4), uKhahlamba Basalt Grassland (Gd 7), Lesotho Highland Basalt Grassland (Gd 8); also Northern Drakensberg Highland Grassland (Gd 5), Drakensberg Foothill Moist Grassland (Gs 10) (Sub-Escarpment Grassland (Gs), Drakensberg Grassland (Gd)), (Grassland Biome).

Assessment rationale: EOO = 18 000 km²; (includes N record, black square); validated EOO much smaller along the Drakensberg of the Lesotho/South Africa border; however, validated range in Drakensberg grasslands mostly protected; therefore, assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by taxonomic revision and a quantitative survey to ascertain the true EOO, AOO and ecological associations; most of the validated range is protected in the uKhahlamba Drakensberg Park (World Heritage Site).

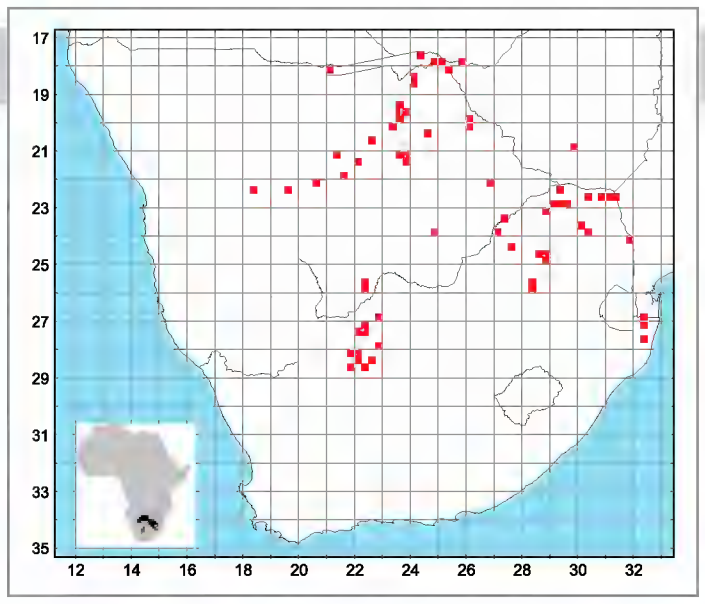
Scarabaeus zambesianus

Péringuey, 1901

= *Scarabaeus arrowi* Gillet, 1911

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: *S. zambesianus*: 'Southern Rhodesia (Victoria Falls)' [Zimbabwe]; *S. arrowi*: 'Lac Ngami, P. B. Spei' [Lake Ngami, Botswana; Northern Cape, South Africa].

Taxonomy: Accepted species.

Distribution: Deep sand areas in dry to moist, southern African, woodland savanna: N South Africa, NE Namibia, Botswana, Zimbabwe; also reported from Mozambique, Angola; report from Somalia is an error and would probably equate to the recently described *S. karlwerneri* Nicolas & Moretto, 2002.

Locality data (mean ± SD, range): Altitude: 947 ± 313, 55–1 958 m; annual rainfall: 445 ± 146, 216–781 mm; annual temperature (max. + min. /2): 20.7 ± 1.7, 14.3–23.7°C (N=100).

Habitat: In uMkhuze Game Reserve: extreme bias to wooded deep sand (deep sand: 43.0, sand over clay: 1.3, sandy clay loam: 0, clay: 0); supported by DBRU collection records: sand (7), sandy loam (2) in shrubland (4) or open woodland (4).

Food types: In Botswana: primarily sampled to dung (pig: 340, elephant: 255, cattle: 137, sheep: 445), few to carrion (chicken livers: 7); DBRU collection records on various dung types: human/cattle mix (1), elephant (2), rhinoceros (1), horse (2), cattle (6).

Temporal activity: Flight activity in darkness during the summer rainy season (Oct. to Apr.); attracted to light; uses polarised light around the moon to orientate during ball-rolling in darkness.

Ecoregions Namibia, Botswana, Zimbabwe: Moister parts of Kalahari Xeric Savanna (AT1309), Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian and Mopane Woodlands (AT0725), Zambezian Baikiaea Woodlands (AT0726), Southern African Bushveld (AT0717).

Bioregions South Africa: W Eastern Kalahari Bushveld (SVk), Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 579 415 km²; the AOO would be smaller due to soil and possible vegetation specialisation; however, shows widespread occurrence in farm rangeland and reserves; clearance of woodland might be detrimental, but no quantitative support; in the SW: sand patches occur in drier areas used primarily for grazing of livestock where transformation is low (0–2 %, W SVk); in the NE: sand patches coincide with more threatened vegetation units (0–58% (SVl), 2–49% (SVcb), 0–20% (SVmp)); however, wide EOO with generalist dung associations currently warrants an assessment as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on vegetation associations, particularly data on possible effects of woodland clearance on sand; protected in uMkhuze Game Reserve, Kruger National Park (South Africa), Chobe National Park (Botswana).

Genus *Sceliages* Westwood, 1837b

Type species and designation: *Ateuchus adamastor* Le Peletier de Saint Fargeau & Serville, 1828, by monotypy.
Synonyms: = *Parascarabaeus* Balthasar, 1961b: Type species: *Scarabaeus* (*Parascarabaeus*) *tonkineus* Balthasar, 1961b, by original designation.
Last review: Entire genus reviewed by Forgie et al. (2002).

The long-established genus, *Sceliages* Westwood, 1837b, was recently reduced to subgeneric status by Forgie et al. (2005). However, as it forms a distinct clade in a molecular/morphological phylogeny (Forgie et al. 2006) and shows specialist behaviour in the use of millipede body contents for breeding (Forgie et al. 2002), there is a strong case for revalidation at generic level (Deschodt et al. 2015b). Accordingly, it is treated as a full genus here.

The genus currently comprises seven closely related species that are restricted to southern Africa. Six of these species are found S of 15°S. They are centred on E savanna (2), Maputaland (1), S Cape and Highveld (1), SW Kalahari (1), and W Cape coast (1). Four species are characteristic of deep sands. All but one are currently assessed as Least Concern (LC) although all are only sporadically collected, probably due to their specialised habits. Further ecological data would be desirable for all species to assist assessment of conservation status.

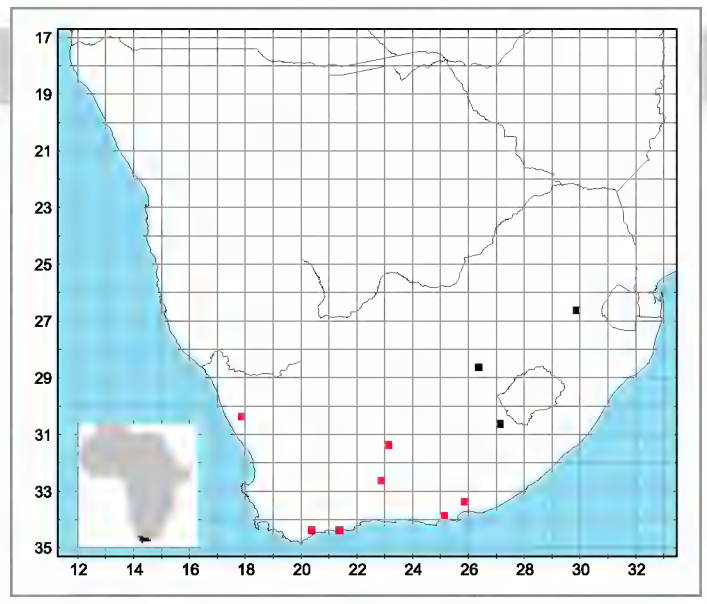
Sceliages adamastor

(Le Peletier & Serville, 1828)

= *Sceliages iopas* Westwood, 1837b
= *Sceliages curvipes* Gillet, 1911
= *Sceliages jopas* Westwood, 1837b, *sensu* zur Strassen, 1965

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: As *Ateuchus adamastor*: 'Cap de Bonne-Espérance' [Cape of Good Hope, South Africa], neotype: 'De Hoop Nature Res.' [South Africa]; *S. iopas*: 'Africa Austral' [southern Africa]; *S. curvipes*: 'Prom. bon. Spei' [Cape of Good Hope]; *S. jopas sensu* zur Strassen: Misspelling of *S. iopas*.

Taxonomy: Accepted species.

Distribution: Primarily, S coast and inland areas of winter and bimodal rainfall regions, South Africa (red squares); doubtful localities in summer rainfall region (black squares).

Locality data (mean ± SD, range): Altitude: 339 ± 453, 3–1 226 m; annual rainfall: 337 ± 122, 132–438 mm; annual temperature (max. + min. /2): 17.3 ± 0.9, 15.3–18.2°C (N=8, red squares only).

Habitat: No quantitative assessment; no recorded data, but collecting localities map onto shrubland vegetation units on both sandy and finer-grained soils.

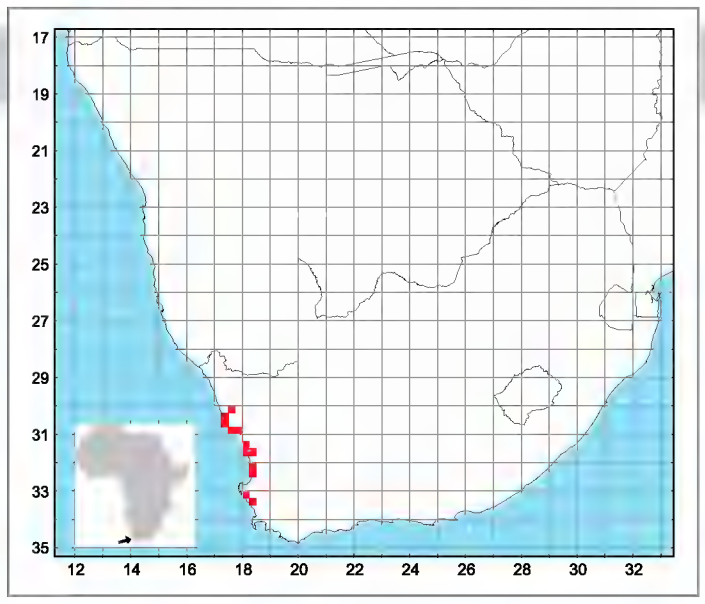
Food types: No quantitative assessment; neotype sampled using a millipede-baited pitfall trap; observed to relocate and bury portions of dead millipedes.

Temporal activity: Diurnal flight activity during spring rainfall peaks with activity extending into summer (Sept. to Feb.).

Bioregions South Africa: Occurrence scattered across vegetation units in Fynbos Biome: De Hoop Limestone Fynbos (FFl 2); Canca Limestone Fynbos (FFl 3); others in Nama Karoo Biome: Eastern Upper Karoo (NKu 4); Gamka Karoo (NKl 1); still others in Succulent Karoo Biome: Namaqualand Klipkoppe Shrubland (SKn 1); also in Algoa Dune Strandveld (AZs 1).

Assessment rationale: EOO = 174 095 km^2 (range defined by red squares only); impossible to adequately assess conservation status as validation of EOO and AOO is required; locality data suggest a widely ranging soil generalist in arid to dry areas supporting natural shrubland plant assemblages, but quantitative support is lacking; sampling of neotype to millipede bait supports specialist food association; currently, assessed as Data Deficient (DD).

Conservation measures: To adequately assess conservation status, a quantitative survey is required to validate the EOO and determine the AOO plus ecological associations; protected along with millipedes in De Hoop Nature Reserve, Western Cape and Addo Elephant National Park, Eastern Cape (South Africa).



Sceliages brittoni

zur Strassen, 1965

No synonyms

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Süfafrika, westl. Kap-Provinz, Umgebung von Leipoldtville, Clanwilliam Distr.' [environs of Leipoldtville, Western Cape, South Africa].

Taxonomy: Accepted species.

Distribution: W coastal deep sands of the winter rainfall region, South Africa.

Locality data (mean ± SD, range): Altitude: 100 ± 98, 0–368 m; annual rainfall: 199 ± 88, 103–378 mm; annual temperature (max. + min. /2): 17.2 ± 1.1, 15.4–18.5°C (N=17).

Habitat: No adequate quantitative data; sampled in low numbers on deep sand in natural shrubland at farms Modderrivier and Geelbek, not in adjoining sparse grassland cleared of shrubs on Geelbek (now part of West Coast National Park where grassland has been permitted to regenerate to natural shrubland).

Food types: No adequate quantitative data; at Farm Geelbek: only sampled by a single cattle dung-baited pitfall trap that also contained millipedes.

Temporal activity: Diurnal flight activity during spring of the winter rainy season (Aug., Sept.) and in early summer (Dec.); possibly shows a strategy of activity by mature adults in spring and emergence of the teneral F1 generation in early summer like some other winter rainfall endemics.

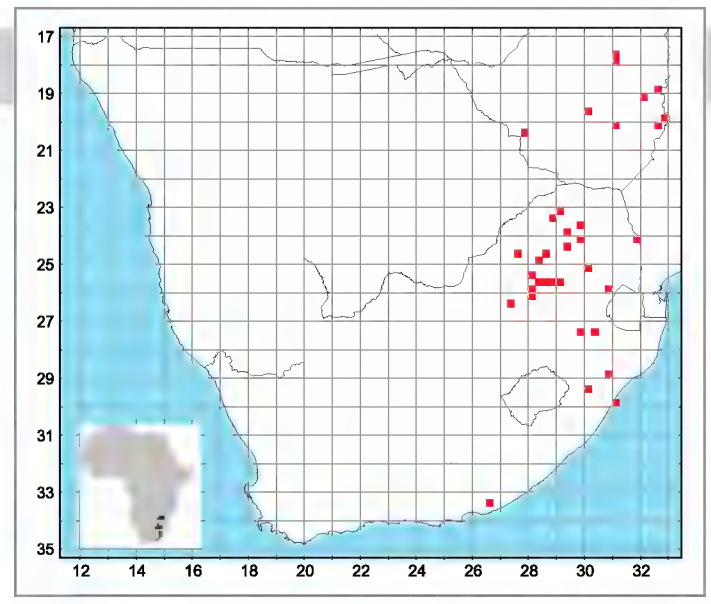
Bioregions South Africa: Vegetation units mostly on deep sand: Namaqualand Strandveld (SKs 7), Namaqualand Coastal Duneveld (SKs 8) (Succulent Karoo Biome); Namaqualand Sand Fynbos (FFd 1), Lamberts Bay Strandveld (FS 1), Langebaan Dune Strandveld (FS 5), Leipoldtville Sand Fynbos (FFd 2), Swartland Granite Renosterveld (FRg 2) (Fynbos Biome).

Assessment rationale: EOO = 6 180 km^2; limited data suggest a soil, vegetation and food type specialist whose AOO might be negatively influenced by habitat transformation on deep coastal sands, which is extensive in the S of its range (25–55%: FS 1, FS 5, FFd 2), but low in the N (8–10%: SKs 7, SKs 8); currently assessed as Least Concern (LC) although small range and exploitation pressures might warrant an IUCN threat category of Near Threatened (NT) in the future.

Conservation measures: Assessment of conservation status would be improved by further quantitative data to support ecological associations; protected in West Coast National Park and the private Grotto Bay Nature Reserve, Western Cape; also in the coastal portion of Namaqua National Park, Northern Cape (South Africa).

Sceliages difficilis

zur Strassen, 1965



No synonyms

Global: LC (see IUCN Red List – LC as *Scarabaeus*)

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Südafrika, östl. Kap-Provinz, Grahamstown' [Grahamstown, Eastern Cape, South Africa].

Taxonomy: Accepted species, but extremely close to *S. gagates* Shipp, 1895.

Distribution: Mainly moderate-altitude, moist savannas of SE Africa: South Africa, Zimbabwe.

Locality data (mean ± SD, range): Altitude: 1 206 ± 387, 1–2 231 m; annual rainfall: 734 ± 168, 519–1 171 mm; annual temperature (max. + min. /2): 18.0 ± 2.2, 11.1–22.5°C (N=41).

Habitat: No quantitative assessment; a single DBRU collection record from grassland within bushveld on deep sand.

Food types: No quantitative assessment; currently, no published records of the use of millipedes as food and breeding resource.

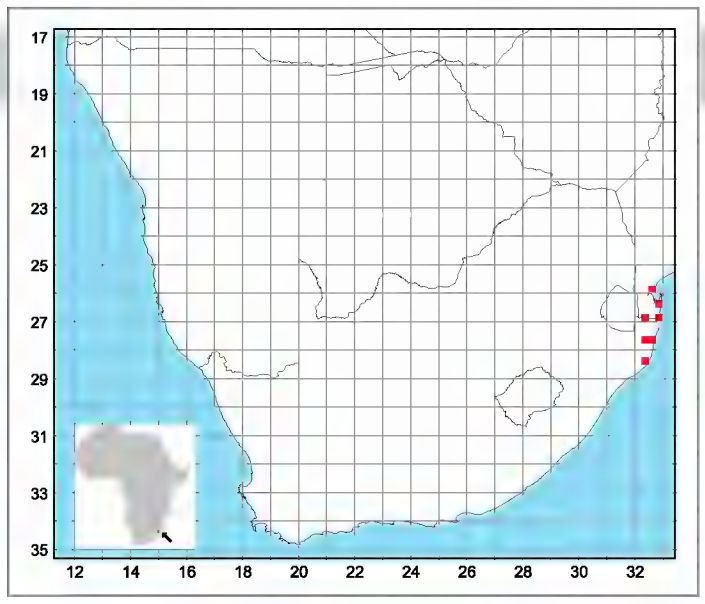
Temporal activity: Diurnal flight activity in the summer rainy season and early dry season (Sept. to June).

Ecoregions Zimbabwe: Southern Miombo Woodlands (AT0719), margins of two other ecoregions.

Bioregions South Africa: Primarily Central Bushveld (SVcb) (Savanna Biome) to extreme margins of Mesic Highveld Grassland (Gm) (Grassland Biome); also margins of Sub-Escarpment Savanna (SVs) to Sub-Escarpment Grassland (Gs).

Assessment rationale: EOO = 214 130 km^2; currently assessed as Least Concern (LC) on basis of large range; however, nothing known about habitat associations; a range centred on bushveld and miombo woodland suggests association with woody savanna within which millipedes have been observed to retreat into thickets during unfavourable conditions; thus, clearance of woody vegetation could be a threat although quantitative support is currently lacking.

Conservation measures: Assessment of conservation status would be much improved by quantitative data on ecological associations, particularly if woodland clearance influences AOO or population density of both *S. dificilis* and millipedes; protected in various nature reserves including: Blouberg, Abe Bailey, Nylsvlei (South Africa); Lake Mutirikwe Game Reserve (Zimbabwe).



Sceliages gagates

Shipp, 1895a

No synonyms

Global: LC (see IUCN Red List – LC as *Scarabaeus*)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: 'Limpopo River' [southern Africa], neotype: 'Sodwana Bay, Natal (3 km from camp)' [South Africa].

Taxonomy: Accepted species, but extremely close to *S. difficilis* zur Strassen, 1965.

Distribution: Deep E coastal sands: NE South Africa, SE Mozambique.

Locality data (mean ± SD, range): Altitude: 31 ± 25, 0–64 m; annual rainfall: 778 ± 98, 654–971 mm; annual temperature (max. + min. /2): 22.4 ± 0.6, 21.8–23.8°C (N=11).

Habitat: No quantitative assessment; most localities coincide with coastal deep sands; on deep sands in Maputo Special Reserve, Mozambique: a single individual recorded in grassland, none recorded in forest patches.

Food types: No quantitative assessment: currently, no published records of use of millipedes as food and breeding resource.

Temporal activity: Diurnal flight activity during the summer rainy season (Oct. to Mar.).

Ecoregions Mozambique: Maputaland Coastal Forest Mosaic (AT0119), Southern Zanzibar-Inhambane Coastal Forest Mosaic (AT0128) (not shown on map).

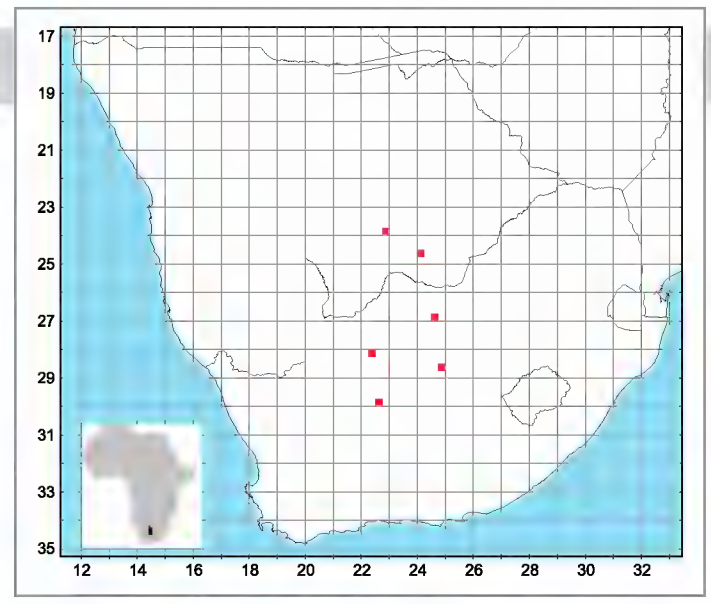
Bioregions South Africa: N Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 13 335 km^2; known EOO comparatively small; ecological data insufficient to determine if AOO would be appreciably smaller; assessed as Least Concern (LC) in line with IUCN Red List, but essentially Data Deficient (DD).

Conservation measures: Assessment of conservation status would be much improved by quantitative data on ecological associations; protected in Maputo Special Reserve (Mozambique) and iSimangaliso Wetland Park (World Heritage Site) (South Africa).

Sceliages granulatus

Forgie & Scholtz, 2002

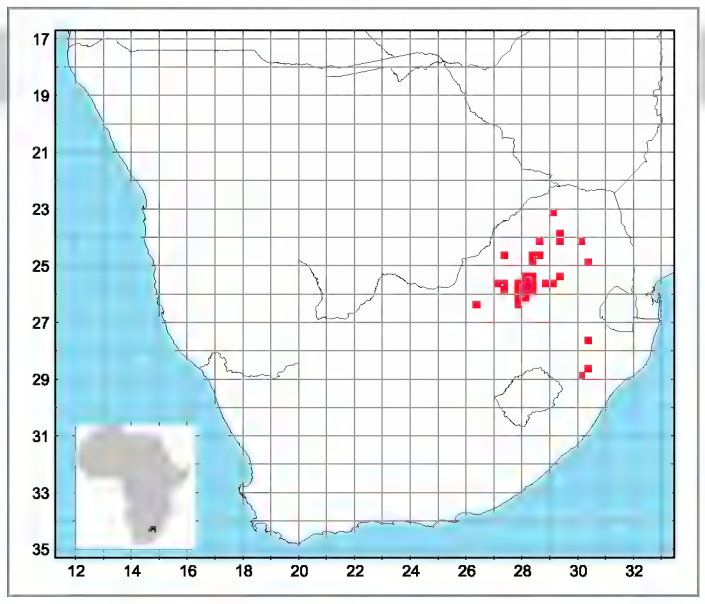


No synonyms

Global: LC
Endemic: RSA, Botswana

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Botswana: Kang, 35 km SE'.
Taxonomy: Accepted species.
Distribution: Arid to dry, deep S Kalahari sands: South Africa, Botswana.
Locality data (mean ± SD, range): Altitude: 1 167 ± 80, 1 102–1 331 m; annual rainfall: 352 ± 75, 223–455 mm; annual temperature (max. + min. /2): 18.9 ± 0.9, 18.0–20.1°C (N=7).
Habitat: No quantitative assessment; limited DBRU collection records all from deep sand (3) in grassland/pasture (2) or shrubland (1).
Food types: No quantitative assessment; limited DBRU collection records all from dead millipedes (3) either from field collection or baited pitfall traps.
Temporal activity: Diurnal flight activity during the summer rainy season (Oct. to Feb.).
Ecoregions Botswana: SE Kalahari Xeric Savanna (AT1309).
Bioregions South Africa: Eastern Kalahari Bushveld (SVk) (Savanna Biome); NE Bushmanland (NKb) (Nama Karoo Biome).
Assessment rationale: EOO = 109 200 km²; soil and food type specialist in an area that is dominated by the preferred deep sands although that association has not been tested quantitatively; range used, mostly, for grazing of domestic livestock; little transformation, except in the SE (18%, SVk 4); assessed as Least Concern (LC).
Conservation measures: Assessment of conservation status would be improved by quantitative data on habitat associations; no known localities in protected areas, but no conservation measures recommended due to sizeable, little-transformed range.



Sceliages hippias

Westwood, 1844

= *Ateuchus microcephalus* Boheman, 1857

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *S. hippias*: 'Africâ meridionali' [southern Africa]; *A. microcephalus*: 'Caffraria interiore' [interior of SE South Africa].
Taxonomy: Accepted species.
Distribution: Centred on moderate-altitude, bushveld savanna in N South Africa.
Locality data (mean ± SD, range): Altitude: 1 302 ± 226, 600–1 702 m; annual rainfall: 680 ± 60, 549–828 mm; annual temperature (max. + min. /2): 17.9 ± 1.3, 15.1–20.4°C (N=41).
Habitat: No quantitative assessment; no data available.
Food types: No quantitative assessment; observed to relocate whole or portions of dead millipedes (two species of Spirostreptidae) for burial in Rustenburg Nature Reserve; attracted to traps baited with either live millipedes or paper exposed to quinone-based secretions of millipedes.
Temporal activity: Diurnal flight activity primarily in the summer rainy season (Sept. to May).
Bioregions South Africa: Primarily Central Bushveld (SVcb), also N Sub-Escarpment Savanna (SVs) (Savanna Biome); extreme margins of three adjoining bioregions in Grassland Biome.
Assessment rationale: EOO = 103 400 km^2; currently assessed as Least Concern (LC) on basis of fairly large range; however, nothing known about habitat associations although centring of range on bushveld suggests association with woody savanna within which millipedes have been observed to retreat into thickets during unfavourable conditions; thus, clearance of woody vegetation could be a threat although quantitative support is required, particularly in SVcb vegetation units where transformation is extensive (up to 49%).
Conservation measures: Assessment of conservation status would be improved by quantitative data on habitat associations of both millipedes and *S. hippias*; protected in Telperion, Loskop Dam, Rustenburg and Tswaing nature reserves (South Africa).

TRIBE SISYPHINI

Mulsant, 1842

As Sisyphaires; Type genus: As *Sisyphe* Latreille, 1807, but prevailng usage, *Sisyphus* Latreille, 1807.

The tribe Sisyphini is probably monophyletic with an old history. It shows quite different morphology and behaviour to other ball-rolling taxa. However, molecular phylogenies suggest close affinities to the ball-rolling canthonine genus, *Epirinus* Dejean, 1833 (Tarasov & Dimitrov 2016). Therefore, they removed *Epirinus* from the polyphyletic tribe, Deltochilini/Canthonini and incorporated it into the tribe Sisyphini Mulsant, 1842, as the tribe Sisyphini *sensu novo*. However, based on evidence offered in a subsequent study, Daniel et al. (2020) removed *Epirinus* to its own tribe, Epirinini van Lansberge, 1874a.

As previously defined, the Sisyphini *s. str.* comprise only three genera showing combined distributions centred primarily on Afro-Eurasia with outliers in central America and on the island of Mauritius. More precisely, *Nesosisyphus* Vinson, 1946, comprises four species endemic to Mauritius. The other two genera (*Sisyphus* Latreille, 1807; *Neosisyphus* Müller, 1942) are widespread in forests, savannas, grasslands and winter rainfall shrublands of the Afrotropical and Oriental regions with *Sisyphus* also present in the Palaearctic and N Neotropical regions.

Daniel et al. (2020) have recently reduced the Sisyphini to two genera (*Nesosisyphus* Vinson, 1946 and *Sisyphus* Latreille, 1807) with *Sisyphus* comprising three subgenera (*Sisyphus* Latreille, 1807; *Parasisyphus* Barbero, Palestrini & Zunino, 1991; *Neosisyphus* Müller, 1942). However, as this revision was unpublished at the time of writing, this book uses the pre-2019 classification system, but with the changes of Daniel et al. (2020) noted in genus or species accounts.

Both *Sisyphus* Latreille, 1807, and *Neosisyphus* Müller, 1942, are widespread in South Africa, with species also found in N Botswana and N Namibia. They do not occur across most of the S Kalahari deep sands or in most of the SW Arid region.

(1) *Neosisyphus* Müller, 1942: Represented by 11 species with distributions centred on winter and bimodal rainfall shrubland (1), Upper Karoo (1), upland grassland (2), E savanna (7), two in shade.

(2) *Sisyphus* Latreille, 1807: Represented by 15 currently validated species with distributions centred on the bimodal rainfall region (1), upland grassland (3), all savanna (2), W savanna (1), E savanna (7), E forest (2), seven in shade. No accounts provided for three new species from South Africa or Eswatini (Daniel et al. 2018) (see Preamble).

Most species are widespread and abundant and do not face serious threats. However, those centred in E coast forest are less secure and one has been assessed as Near Threatened (NT).

Genus *Neosisyphus* Müller, 1942

(recent status change: subgenus of *Sisyphus* Latreille, 1807)

Type species and designation: *Sisyphus atratus* Klug, 1855, by original designation.
Synonyms: None.
Last review: Afrotropical species revised by Montreuil (2015a) with the addition of eight new species; new southern African species added by Daniel et al. (2018); *Neosisyphus* has become a subgenus of *Sisyphus* Latreille, 1807 (Daniel et al. 2020).

Neosisyphus Müller, 1942, was formally raised to full genus only recently (Montreuil 2015a) having been described as a subgenus of *Sisyphus* Latreille, 1807. Although *Neosisyphus* retained its generic status when the book was completed at the end of 2017, the phylogeny of Daniel et al. (2020) again reduces it to a subgenus of *Sisyphus* Latreille (1807). In Montreuil's review (2015a), species revision and cited distributions of the *N. barbarossa* species group differ to those of a previous unpublished review of southern African *Neosisyphus* (Paschalidis 1974a). Using more detailed southern African data, the species identities and distributions cited here for the *barbarossa* group follow those of Paschalidis.

Neosisyphus currently comprises 33 species widely distributed in the savannas of Africa (31) with limited representation in the Oriental region (2). In southern Africa, *Neosisyphus* is represented by 11 species distributed between five groups with different behavioural patterns. They mostly show widespread distributions centred on moister E and S regions.

Many *Neosisyphus* species are widespread in farm pastures and rangeland on dung of domestic livestock. They would face few threats at present. Therefore, nine have been assessed as Least Concern (LC) although two are assessed as Data Deficient (DD).

Group patterns in southern Africa: Group designations are based on Montreuil (2015a).

Group *barbarossa*: Three species centred in E highlands, moist E savanna or dry E savanna in which the egg is laid before burial of the brood ovoid.

Group *quadricollis*: Two species centred dry E highland grasslands or Upper Karoo and SW coastal shrubland in which the egg is laid before burial of the brood ovoid.

Group *rubrus*: Two species centred on E savanna and moist upland grassland or on dry upland grassland in which the egg is laid after burial of the ball, which has a protuberance above the egg chamber.

Group *spinipes*: Three E savanna-centred species with shade, open woodland or grassland bias, two distributed into the tropics, brood balls have a large protuberance above the egg chamber, they are attached to grass stalks or twigs, or abandoned on the soil surface.

Group *tibialis*: One E coastal shade species in which the egg is laid after burial of the ball, which has a protuberance above the egg chamber.

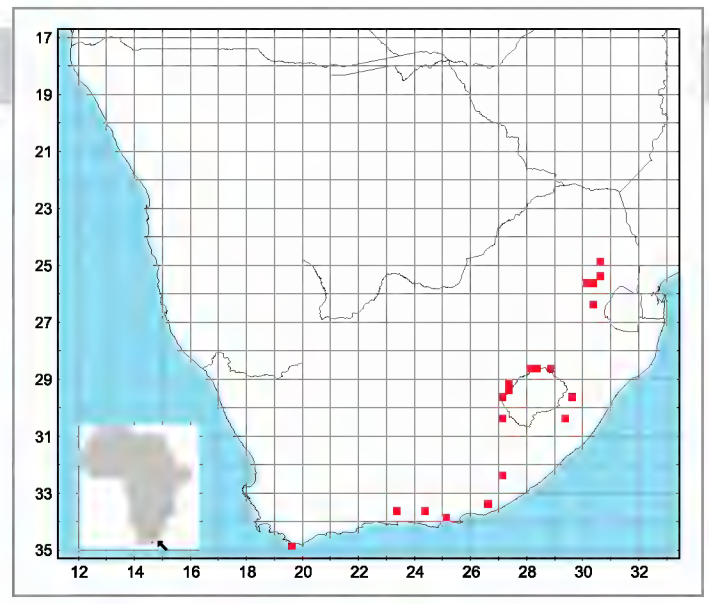
Neosisyphus barbarossa

(Wiedemann, 1823) (but see Taxonomy)

= *Sisyphus rugosus* Gory, 1833

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: As *Sisyphus barbarossa*: 'Prom. bon. sp.' [Cape of Good Hope, South Africa]; *S. rugosus*: 'Cap B.-Esp.' [Cape of Good Hope, South Africa], lectotype: No locality stated.

Taxonomy: Accepted species (recent status change: genus *Sisyphus* Latreille, 1807; subgenus *Neosisyphus* Müller, 1942), but interpretation differs to both the unpublished revision of southern African Sisyphini (Paschalidis 1974a) and the published revision of Afrotropical *Neosisyphus* (Montreuil 2015a); both authors cite *S. rugosus* as a synonym; further study is required to determine if the lectotype created for *S. rugosus* is truly a synonym of *N. barbarossa* (Wiedemann), which was not seen by Montreuil; limited sexual dimorphism (legs).

Distribution: South Africa; in the N: cool moist highlands along NE edge of E escarpment encompassing the Lesotho highlands (1 677 ± 246 m, N=19); in the S: descending to lowlands along the S Cape coastline (441 ± 321 m, N=5); this distribution is consistent with that cited by Pascahalidis (1974), but differs radically to that cited by Montreuil (2015a).

Locality data (mean ± SD, range): Altitude: 1 408 ± 581, 110–2 199 m; annual rainfall: 682 ± 158, 360–958 mm; annual temperature (max. + min. /2): 14.7 ± 1.6, 11.2–17.4°C (N=23).

Habitat: No quantitative assessment; DBRU collection records from sand (3), sandy loam (3), sandy clay loam (6) in grassland/pasture (8) or a fallow crop field (1).

Food types: No quantitative assessment; DBRU collection records entirely from cattle dung (13).

Temporal activity: Diurnal flight activity, primarily during the summer rainy season in the N (Oct. to Apr.); recorded in Apr. in the bimodal rainfall region.

Bioregions South Africa: In the N: higher parts of E Mesic Highveld Grassland (Gm), W Sub-Escarpment Grassland (Gs) (Grassland Biome); on the S coast: cleared patches in Albany Thicket Biome (AT) and vegetation units in Renosterveld (Fynbos Biome).

Assessment rationale: EOO = 27 150 km^2; widely distributed and readily attracted to dung of domestic livestock in farmland; however, vegetation units in N highland range threatened by transformation, particularly cultivation or forest plantations (transformation in Mpumalanga range: 22–23%, Gm 18, Gm 21; Lesotho border range: 33–50%, Gm 1, Gm 4); unclear if S Cape pasture records reflect natural occurrence or are due to range expansion in response to clearance of natural shrubland; currently assessed as Least Concern (LC) on basis of relatively large range.

Conservation measures: Correct assessment of conservation status is dependent on revision and validation of taxonomic identity and geographical range; assessment would be improved by quantitative data on ecological associations, particularly effects of pasture improvement and transformation of habitats; only a single known locality, Baviaanskloof Nature Reserve (South Africa), occurs within officially protected areas.

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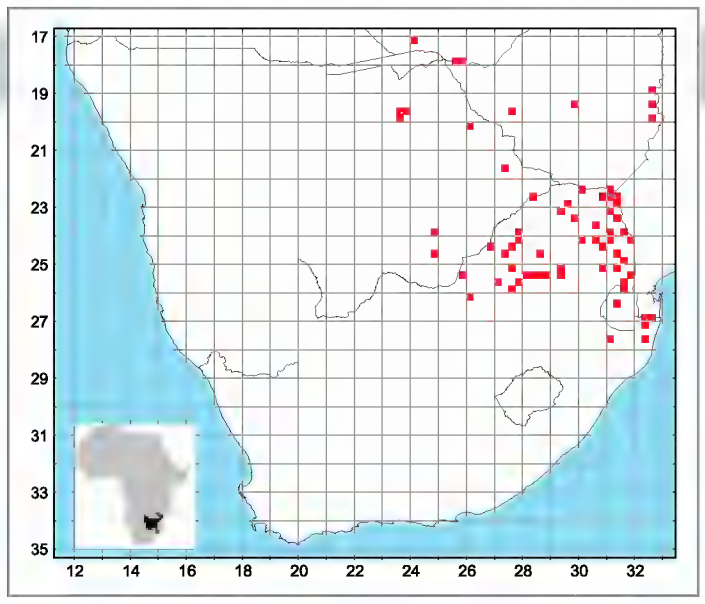


Neosisyphus calcaratus

(Klug, 1855) (but see Taxonomy)

= *Sisyphus rubripes* Boheman, 1857

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Sisyphus calcaratus*: 'Sena' [central Mozambique]; *S. rubripes*: 'Caffraria interiore' [interior of SE South Africa].

Taxonomy: Accepted species (but recent status change: genus *Sisyphus* Latreille, 1807; subgenus *Neosisyphus* Müller, 1942); formerly erroneously synonymised with *Neosisyphus rugosus* (Gory, 1833); valid species status supported by revisions of southern African (Paschalidis 1974a, unpublished) and African Sisyphini (Montreuil 2015a, published); limited sexual dimorphism (legs).

Distribution: Widespread in hot, dry, southern African savanna woodland: South Africa, Eswatini, Botswana, Zimbabwe, Mozambique, Zambia; other citations associated with *N. rugosus* presumably errors: Angola, Democratic Republic of the Congo (DRC), Rwanda, Kenya, Ethiopia.

Locality data (mean ± SD, range): Altitude: 744 ± 422, 41–1 847 m; annual rainfall: 612 ± 152, 306–1 184 mm; annual temperature (max. + min. /2): 21.0 ± 2.1, 14.7–25.7°C (N=86).

Habitat: No adequate quantitative data; in uMkhuze Game Reserve: inconclusive soil data: sand (3.8), duplex soil (sand over clay) (24.3), sandy clay loam (12.3), clay (14.3); DBRU collection records on sand (7), sandy loam (6), sandy clay loam (1), clay (1) with a bias to wooded habits: grassland/pasture (2), shrubland (4), open woodland (8), forest (2).

Food types: At Phalaborwa: readily attracted to dung with bias to cattle (450) as opposed to pig (230) or elephant (130); DBRU collection records from dung of cattle (15), buffalo (2), wildebeest (1), waterbuck (1), elephant (6), rhinoceros (1), horse (1).

Temporal activity: Diurnal flight activity, primarily during the summer rainy season (Oct. to Apr.); at Phalaborwa: more abundant on a warm sunny day soon after heavy rainfall (554) than on a hot sunny day (225) or a warm cloudy day following light rainfall (21).

Ecoregions Botswana, Zimbabwe: Drier areas: Zambezian and Mopane Woodlands (AT0725), Southern African Bushveld (AT0717), margins of Kalahari Xeric Savanna (AT1309), Kalahari Acacia-Baikiaea Woodlands (AT0709), margins of two other ecoregions.

Bioregions South Africa: Central Bushveld (SVcb), Lowveld (SVl), Mopane (SVmp) (Savanna Biome).

Assessment rationale: EOO = 712 200 km^2; AOO would be smaller if associated with woody habitats; proportion of tree clearance unknown, but transformation across South African range varies from 0 to 58% (SVl), 2–49% (SVcb), 0–20% (SVmp); however, widespread and readily attracted to various dung types in both reserves and farmland, so assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by further quantitative data on habitat associations, particularly those with vegetation; protected in Kruger National Park and uMkhuze Game Reserve (South Africa).

Neosisyphus confrater

(Kolbe, 1914) (but see taxonomy)

No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Sisyphus confrater*: 'Bei Bukoba' [near Bukoba, Tanzania].

Taxonomy: Accepted species (but recent status change: genus *Sisyphus* Latreille, 1807; subgenus *Neosisyphus* Müller, 1942); currently synonymised with *Neosisyphus setiger* (Roth, 1851) described from 'Abyssinie' [Ethiopia]; interpreted here according to an unpublished revision of southern African Sisyphini (Paschalidis 1974a); however, species identity of southern African populations needs to be validated by further comparison with types (Tanzania (lectotype male), Ethiopia (holotype female)) and other E African material; formerly synonymised in error with *Neosisyphus armatus* (Gory, 1833), a species now considered to show a W African distribution; limited sexual dimorphism (legs).

Distribution: Moist savanna on SE coast and lower edges of SE uplands of Africa: South Africa, Eswatini, Mozambique, Zimbabwe; putative type locality in Tanzania.

Locality data (mean ± SD, range): Altitude: 687 ± 631, 0–1 890 m; annual rainfall: 892 ± 159, 627–1 247 mm; annual temperature (max. + min. /2): 19.7 ± 3.0, 13.1–25.2°C (N=50).

Habitat: In Ithala Game Reserve: only recorded on sandy loam in grassland (8) at upper edge of escarpment (1 142 m); DBRU collection records biased to finer-grained soils, sand (7), sandy loam (8), sandy clay loam (7), clay (2) in unshaded vegetation, pasture/grassland (25), open woodland (3) forest (1).

Food types: In Ithala Game Reserve: attracted to dung of pig (4), horse (2), cattle (2); DBRU collection records primarily on cattle dung (27) with few on horse (1), elephant (1) or human dung (3).

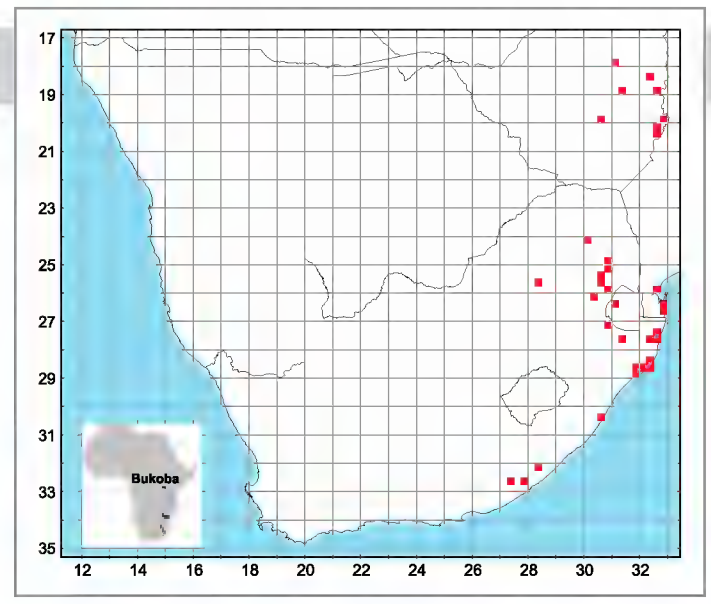
Temporal activity: Diurnal flight activity primarily during the summer rainy season (Sept. to May).

Ecoregions Zimbabwe, Mozambique: Southern Miombo Woodland (AT0719), Eastern Zimbabwe Montane Forest Mosaic (AT1006), Maputaland Coastal Forest Mosaic (AT0119), Southern Zanzibar-Inhambane Coastal Forest Mosaic (AT0128).

Bioregions South Africa: Indian Ocean Coastal Belt Biome (CB) and warmer areas on edge of escarpment in Mesic Highveld Grassland (Gm) (Grassland Biome) bordering Central Bushveld (SVcb) and Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 118 955 km² (range in southern Africa only; putative Bukoba type locality also marked); apparent bias to grassland association may indicate a different species to that described from Bukoba; currently assessed as Least Concern (LC) on the basis of extensive EOO in open vegetation.

Conservation measures: Correct assessment of conservation status is dependent on revision and validation of taxonomic identity and geographical range; assessment would also be improved by further quantitative data on ecological associations; protected in Ithala Game Reserve (South Africa).



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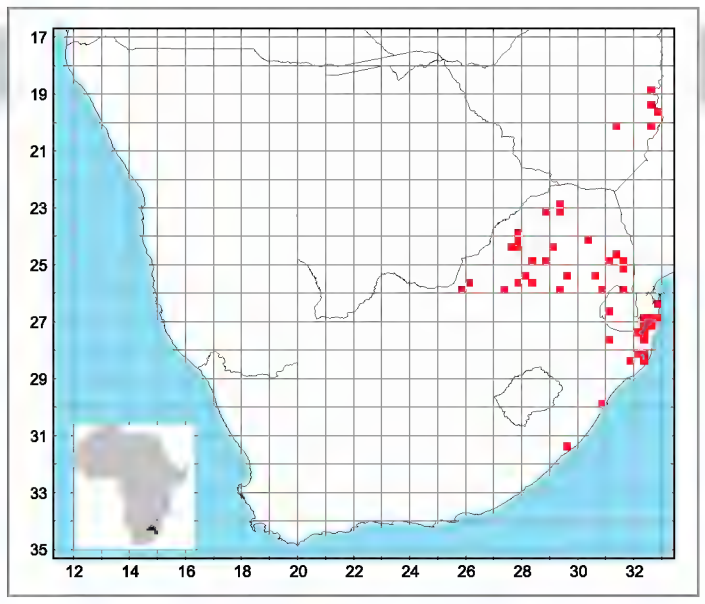


Neosisyphus fortuitus

(Péringuey, 1901) (but see Taxonomy)

No synonyms

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Sisyphus fortuitus*: 'Natal (Durban)' [Durban, KwaZulu-Natal, South Africa].

Taxonomy: Accepted species (but recent status change: genus *Sisyphus* Latreille, 1807; subgenus *Neosisyphus* Müller, 1942); limited sexual dimorphism (legs).

Distribution: Moist, coastal and upland, woodland savanna of SE Africa: N South Africa, E Zimbabwe, Eswatini, S Mozambique; citations from Cameroon and Guinea (Conakry) are errors.

Locality data (mean ± SD, range): Altitude: 748 ± 560, 0–1 613 m; annual rainfall: 746 ± 155, 491–1 188 mm; annual temperature (max. + min. /2): 19.8 ± 2.0, 15.6–22.6°C (N=56).

Habitat: In Gauteng bushveld: moderate bias to deep sand (264) compared to sandy clay loam (97) with strong bias to shaded thicket (252) and open woodland (98) compared to grassland (11); in uMkhuze Game Reserve: 66% of 279 recorded in shade with weak bias to sandy soils, sand (10.8), sand over clay (3.8), sandy clay loam (8.5), clay (3.1); largely supported by DBRU collection records from sand (6), sandy loam (4), sandy clay loam (2) in forest/thicket (4), shrub/woodland (6), grassland (4).

Food types: No quantitative assessment; DBRU collection records on dung of cattle (14), wildebeest (2), rhinoceros (2), elephant (1), horse (1), human (1), human/cattle mix (5).

Temporal activity: Diurnal flight activity, primarily during the summer rainy season (Oct. to June).

Ecoregions Zimbabwe, Mozambique:, Eastern Zimbabwean Montane Forest Grassland Mosaic (AT1006), Maputaland Coastal Forest Mosaic (AT0119)), margins of one other ecoregion.

Bioregions South Africa: Centred on Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome); Indian Ocean Coastal Belt Biome (CB); also extreme margins of adjoining Grassland Biome.

Assessment rationale: EOO = 154 350 km²; AOO centred on woodland savanna owing to habit of abandoning brood balls in the litter under shade offered by shrubs and trees; therefore EOO and AOO would be threatened by clearance of woody vegetation; transformation in vegetation units is 2–49% in SVcb and 0–58% in SVl; however, widespread in N South Africa in both reserves and on farms; currently assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on dung type associations and an appraisal of the occurrence of shaded vegetation across its EOO; protected in uMkhuze, Hluhluwe–iMfolozi and Ithala game reserves (South Africa).

Neosisyphus infuscatus

(Klug, 1855) (but see Taxonomy)

= *Sisyphus atratus* Klug, 1855, *sensu* Péringuey, 1901
= *Neosisyphus bornemisszai* Ferreira, 1972

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Sisyphus infuscatus*: 'Sena', lectotype: 'Sena' [central Mozambique]; *S. atratus sensu* Péringuey: 'Cape Colony (Queenstown)' [Eastern Cape, South Africa]; *N. bornemisszai*: 'Manhoca (Moçambique)' [Mozambique].

Taxonomy: Accepted species (but recent status change: genus *Sisyphus* Latreille, 1807; subgenus *Neosisyphus* Müller, 1942); formerly erroneously synonymised with *Neosisyphus spinipes* (Thunberg, 1818); valid species status supported by revisions of southern African (Paschalidis 1974a, unpublished) and African Sisyphini (Montreuil 2015a, published); limited sexual dimorphism (legs).

Distribution: Dry, hot lowland savanna on the E seaboard from S to E Africa: South Africa, Zimbabwe, Zambia, Mozambique, Tanzania, Kenya.

Locality data (mean ± SD, range): Altitude: 431 ± 392, 0–1 432 m; annual rainfall: 687 ± 221, 306–1 275 mm; annual temperature (max. + min. /2): 21.2 ± 2.4, 15.0–25.7°C (N=56).

Habitat: No adequate quantitative assessment; in uMkhuze Game Reserve: recorded on sand (2.0), duplex soil (sand over clay) (9.3), sandy clay loam (7.5) and clay (4.5); DBRU collection records on sand (9), sandy loam (2), sandy clay loam (8) and clay (4) in grassland (5), shrub/woodland (9) and forest (3).

Food types: At Phalaborwa: stronger association with cattle dung (49) compared to pig (15) or elephant dung (14); DBRU collection records from dung of cattle (19), buffalo (4), wildebeest (1), waterbuck (1), elephant (4), human/cattle dung mix (2).

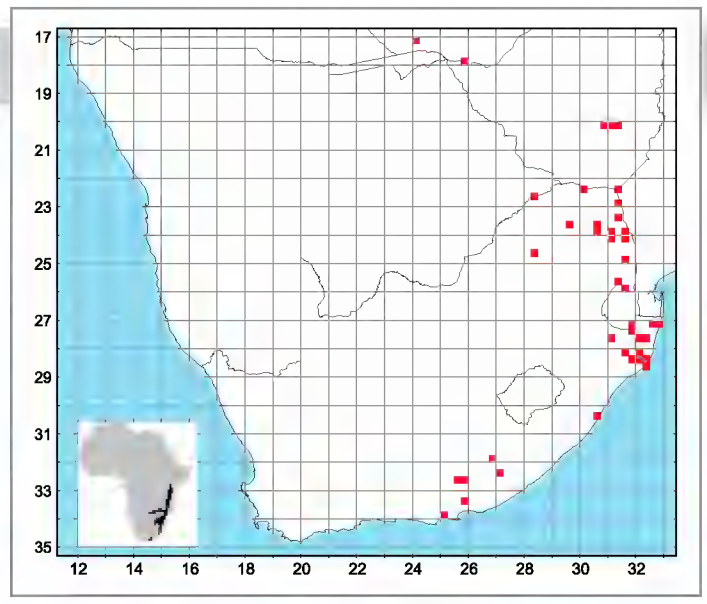
Temporal activity: Diurnal flight activity during the summer rainy season (Oct. to Apr.); also in cooler drier months (Aug., May) in the warmer coastal region of KwaZulu-Natal; at Phalaborwa: abundant both in warm conditions soon after heavy rainfall (42) and in hot, dry conditions (28), but not in warm cloudy conditions soon after light rainfall (2).

Ecoregions Zimbabwe: Zambezian and Mopane Woodlands (AT0725).

Bioregions South Africa: Lowveld (SVl), Mopane (SVmp) (Savanna Biome); drier parts, Indian Ocean Coastal Belt (CB) and Albany Thicket (AT) biomes; marginal in two other bioregions.

Assessment rationale: EOO = 900 785 km² (gross estimate); apparently a soil type generalist, possibly, with a bias to woodland savanna; if so might be influenced by clearance of trees; in the main part of its range in South African savanna, transformation is 0–58% (SVl), 0–20% (SVmp); however, assessed as Least Concern (LC) owing to wide range in dry savanna.

Conservation measures: Assessment of conservation status would be improved by further quantitative data on habitat associations, particularly vegetation associations; protected in the Kruger National Park and uMkhuze Game Reserve (South Africa).



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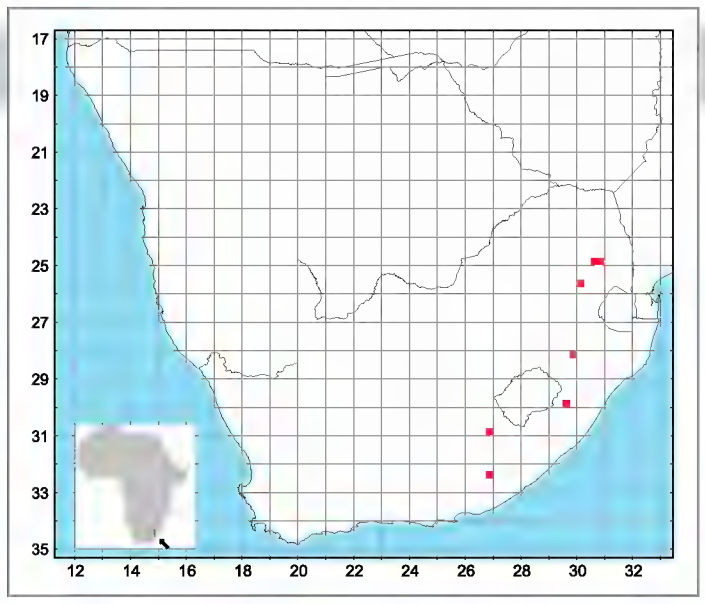


Neosisyphus kuehni

(Haaf, 1955) (but see Taxonomy)

No synonyms

Global: DD (see IUCN Red List – DD)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Sisyphus kühni*: 'Südafrika (Natal, Griqualand)' [KwaZulu-Natal, South Africa].

Taxonomy: Accepted species (but recent status change: genus *Sisyphus* Latreille, 1807; subgenus *Neosisyphus* Müller, 1942); limited sexual dimorphism (legs).

Distribution: Moist upland to highland grassland along middle to upper edge of the E escarpment, summer rainfall region, South Africa.

Locality data (mean ± SD, range): Altitude: 1 646 ± 239, 1 225–1 890 m; annual rainfall: 783 ± 143, 556–996 mm; annual temperature (max. + min. /2): 14.1 ± 1.4, 12.6–17.0°C (N=8).

Habitat: No adequate quantitative assessment; on Farm Boschberg in natural grassland on sandy clay loam: only recorded on Highveld (7, 1 675–1 688 m) not in grassland at base of hill (0, 1 265–1 302 m) limited DBRU collection records from various soil types, sand (1), sandy loam (2), sandy clay loam (1) in grassland/pasture (3).

Food types: No quantitative assessment; limited DBRU collection records all from cattle dung (4).

Temporal activity: Diurnal flight activity, primarily during the summer rainy season (Nov. to May).

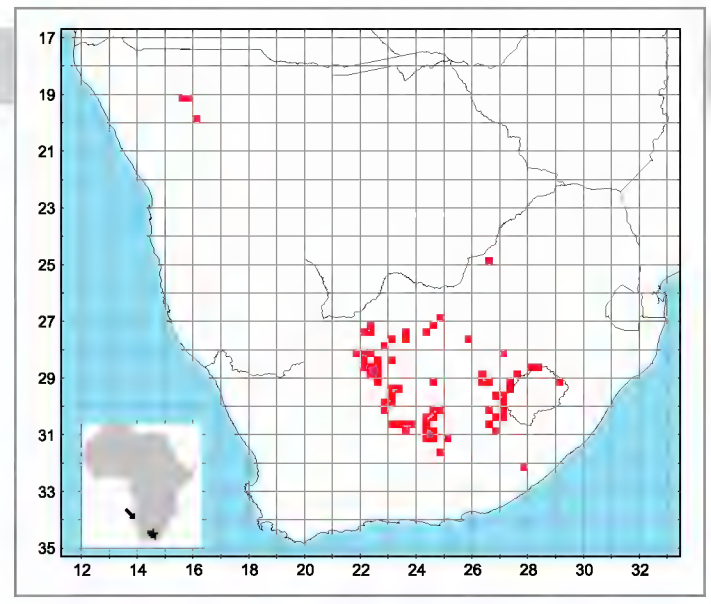
Bioregions South Africa: In the N: Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs); in the S: S Dry Highveld Grassland (Gh), S patch Drakensberg Grassland (Gd) on Amatola Mts (Grassland Biome).

Assessment rationale: EOO = 30 620 km^2; widespread, but poorly known; probably restricted to highland grassland, but quantitative support required; could probably be assessed as Least Concern (LC) on basis of widespread occurrence, but currently assessed as Data Deficient (DD); low numbers in collections could equally be a collection artefact or due to low population density; further study required, particularly considering there is 23–52% habitat transformation around known localities in the N of its range (Gm 18, Gm 22, Gs 8).

Conservation measures: Before conservation status may be adequately assessed, a quantitative survey of highland grassland is required to determine ecological associations and possible effects of habitat disturbance, particularly conversion to arable land, pasture improvement or commercial forestry; not currently known to occur in any protected area.

Neosisyphus macrorubrus

(Paschalidis, 1974b) (but see Taxonomy)



No synonyms

Global: LC (see IUCN Red List – LC)
Endemic: RSA, Namibia

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Sisyphus macrorubrus*: 'Vanstadensrus, O.F.S.' [Free State, South Africa].

Taxonomy: Accepted species (but recent status change: genus *Sisyphus* Latreille, 1807; subgenus *Neosisyphus* Müller, 1942); limited sexual dimorphism (legs).

Distribution: Disjunct pattern: South Africa, Namibia; cool, dry, SW Highveld and arid NE Nama Karoo uplands, South Africa; uncommon outlier presence on uplands of N Namibian plateau.

Locality data (mean ± SD, range): Altitude: 1 295 ± 235, 814–2 392 m; annual rainfall: 366 ± 148, 221–815 mm; annual temperature (max. + min. /2): 16.8 ± 2.2, 9.9–22.2°C (N=129).

Habitat: No adequate quantitative assessment; in Northern Cape: greatest frequency in cooler Upper Karoo (80% of study sites), less in lower-altitude Karoo (14%) and Kalahari (34%), more frequent on sand (1.5/trap, N=75), but similar abundance on sandy loam (2.2, N=29); DBRU collection records from sand (11), sandy loam (12), sandy clay loam (10), clay (2) in grassland/pasture (15), scrub/shrubland (30), open woodland (5).

Food types: No quantitative assessment; most DBRU collection records from cattle dung (41), also zebra (1)

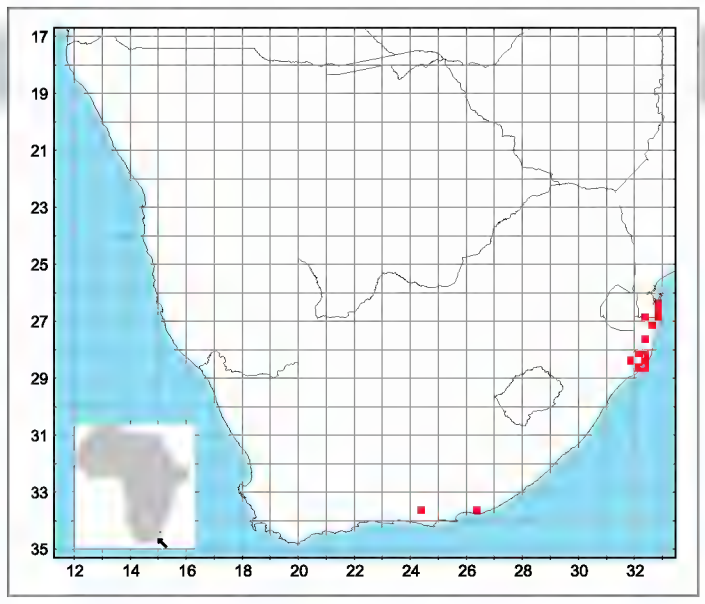
Temporal activity: Diurnal flight activity, primarily during the summer rainy season (Oct. to May).

Ecoregions Namibia: S Angolan Mopane Woodlands (AT0702).

Bioregions South Africa: Cooler S Mesic Highveld Grassland (Gm), Dry Highveld Grassland (Gh) (Grassland Biome); Eastern Kalahari Bushveld (SVk) (Savanna Biome); moister NE Upper Karoo (NKu) (Nama Karoo Biome).

Assessment rationale: EOO = 239 965 km^2; in South Africa: SW limits of distribution centred in an area used primarily for grazing of domestic livestock to whose dung it is readily attracted; E limits more transformed (4–50%, Gh, Gm); although poorly protected in South Africa, little threatened over most of range; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by further quantitative ecological data; protected in Etosha National Park (Namibia) and the private Tswalu Kalahari Reserve (South Africa).



Neosisyphus mirabilis

(Arrow, 1927) (but see Taxonomy)

= *Sisyphus spinipes* Gory, 1833

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: As *Sisyphus mirabilis*: *nom nov.* for *Sisyphus spinipes* Gory: 'Cap B.-Esp.' [Cape of Good Hope, South Africa], lectotype: Not stated.

Taxonomy: Accepted species (but recent status change: genus *Sisyphus* Latreille, 1807; subgenus *Neosisyphus* Müller, 1942); limited sexual dimorphism (legs).

Distribution: Possible disjunction between two centres in coastal lowlands of Maputaland Centre of Endemism and Eastern Cape; South Africa, Mozambique; more northerly distribution on Mozambique coast requires investigation.

Locality data (mean ± SD, range): Altitude: 82 ± 170, 0–762 m; annual rainfall: 825 ± 154, 360–1 010 mm; annual temperature (max. + min. /2): 21.7 ± 1.2, 17.4–22.6°C (N=35).

Habitat: In uMkhuze Game Reserve: bias to deep sand (116.2), but abundant on duplex soil (sand over clay) (29.4), sandy clay loam (11.9) and clay (35.3); on deep sands in Maputo Special Reserve: more abundant in large and medium patches of inland sand forest (4.4, 4.0/trap) than in small patches (0.7) or cooler coastal dune forest (0.5), virtually absent from grassland (0.1); on deep sands at Richards Bay: more abundant in regenerating woodland on mined coastal dunes (12–33 yr) (6.8/trap), rare in deeper shade of natural dune forest (0.02); limited DBRU collection records from sandy clay loam (1) in open woodland (1) and forest (5).

Food types: No quantitative assessment; limited DBRU collection records from horse (1) and a mixture of human and cattle dung (2).

Temporal activity: Diurnal flight activity throughout much of the year in warmer N coastal range (July to May); probably only in warmer summer in Eastern Cape.

Ecoregions Mozambique: Maputaland Coastal Forest Mosaic (AT0119).

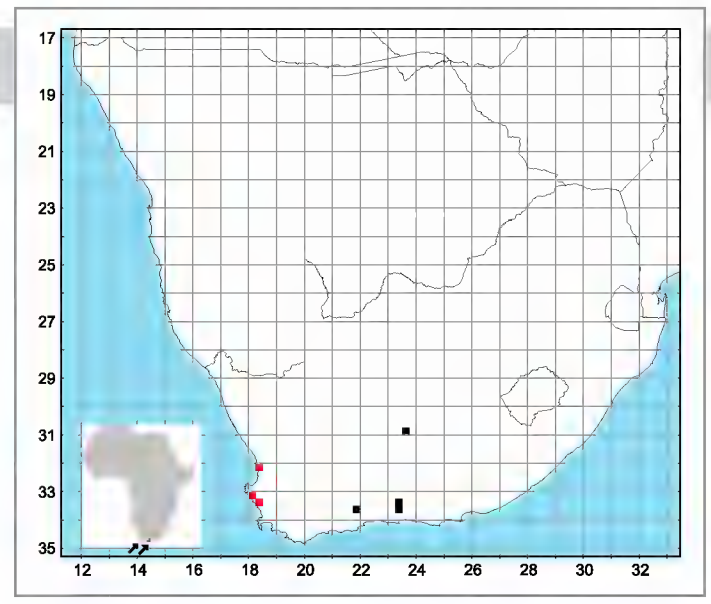
Bioregions South Africa: In KwaZulu-Natal: N Indian Ocean Coastal Belt Biome (CB); also adjoining Lowveld (SVl) (Savanna Biome); in Eastern Cape: Albany Thicket Biome (AT).

Assessment rationale: EOO = 14 150 km^2; AOO more limited due to specialised shade association; protected over about 50% of the known range, but would be negatively influenced by woodland or forest clearance; transformation in Zululand SVl: 22–58%, but assessed as Least Concern (LC) owing to extent of protection.

Conservation measures: Assessment of conservation status would be improved by data on food associations; protection offered over much of the range, particularly in Baviaanskloof Nature Reserve, Hluhluwe–iMfolozi and uMkhuze game reserves (South Africa); Maputo Special Reserve (Mozambique).

Neosisyphus quadricollis

(Gory, 1833) (but see Taxonomy)



No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J	West
J	A	S	O	N	D	J	F	M	A	M	J	East

Type localities: As *Sisyphus quadricollis*: 'Cap B.-Esp.' [Cape of Good Hope, South Africa], lectotype: Not stated.

Taxonomy: Accepted species (but recent status change: genus *Sisyphus* Latreille, 1807; subgenus *Neosisyphus* Müller, 1942); despite ecological differences between W and E populations, now established as a single species (Daniel et al. 2018); limited sexual dimorphism (legs).

Distribution: Possibly disjunct occurrence between dry SW coastal deep sands in Western Cape (red squares) and dry fynbos and Karoo of Eastern Cape (black squares), South Africa.

Locality data (mean ± SD, range): West: average altitude: 32 ± 13, 15–45 m; average annual rainfall: 282 ± 63, 191–326 mm; average annual temperature (max. + min. /2): 16.5 ± 1.0, 15.7–17.9°C (N=4). East: average altitude: 1 072 ± 235, 868–1 392 m; average annual rainfall: 314 ± 38, 270–363 mm; average annual temperature (max. + min. /2): 14.9 ± 0.2, 14.7–15.1°C (N=4).

Habitat: No adequate quantitative assessment; W populations on W coast deep sands in natural shrubland (23); in the W, not recorded on finer-grained soils or in pastures cleared of natural shrubland; E populations on sandy loam in Karoo grassland, also sand and clay soil areas in E Fynbos-Renosterveld Bioregion.

Food types: No quantitative assessment; sampled to cattle dung and cattle/sheep mixture.

Temporal activity: Diurnal flight activity; in the winter rainfall region: West Coast populations on farms Modderrivier and Pampoenvlei show spring activity declining into early summer (Oct., 13; Nov., 8; Dec., 2); in the bimodal rainfall region: records are only from late summer (Jan. to March).

Bioregions South Africa: Vegetation units in the W: West Strandveld (FS 1, FS 5), Atlantis Sand Fynbos (FFd 4); in the E: Uniondale Shale Renosterveld (FRs 16), South Rooiberg Sandstone Fynbos (FFs 22) (Fynbos Biome); one E record in Upper Karoo (NKu) (Nama Karoo Biome).

Assessment rationale: EOO = 2 750 km² (W), 23 050 km² (E); W and E populations apparently differ in seasonal activity, altitude and temperature range in similarly dry areas; most records from areas of Fynbos in winter and bimodal rainfall regions with one record from Nama Karoo in the late summer rainfall region; W populations face threats as they occupy a small range in areas that are 25–40% transformed; however, many contradictions in existing data; currently assessed as Data Deficient (DD).

Conservation measures: Assessment of conservation status would benefit from a survey to establish the full EOO and AOO as well as quantitative data on ecological associations in both W and E populations; no current records known from officially protected areas although the coastal part of Modderrivier is now in the private Grotto Bay Nature Reserve.

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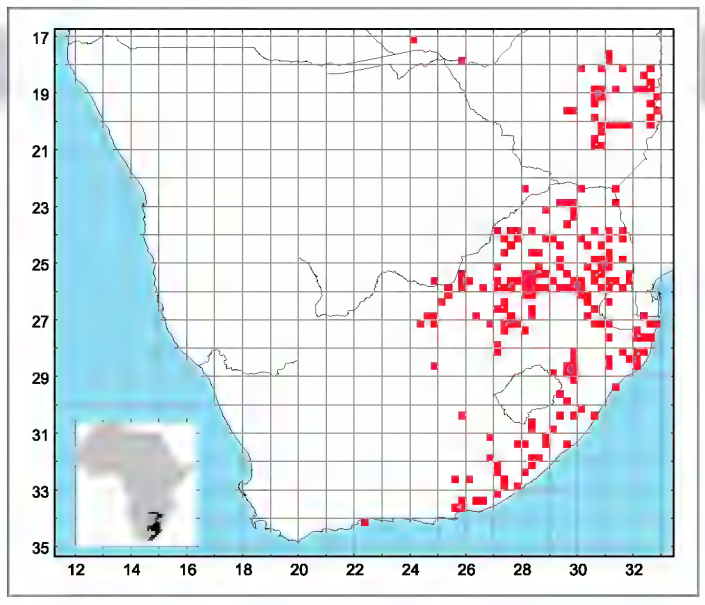

Neosisyphus rubrus

(Paschalidis, 1974b) (but see Taxonomy)

No synonyms

Global: LC (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Sisyphus rubrus*: 'Castle Gorge, Tvl. 42 mi W [of] Pretoria' [North-West Province, South Africa].

Taxonomy: Accepted species (but recent status change: genus *Sisyphus* Latreille, 1807; subgenus *Neosisyphus* Müller, 1942); misidentified by Péringuey (1902), as *S. rubripes* Boheman, 1857; re-described by Haaf (1955), as *S. rubripes* Péringuey, a pre-occupied name, thus, invalidating the lectotype designated from Péringuey's material; limited sexual dimorphism (legs).

Distribution: Warmer areas of upland grassland; also moist, SE African open savanna woodland: South Africa, E Botswana, Zimbabwe, Zambia, Mozambique.

Locality data (mean ± SD, range): Altitude: 1 067 ± 461, 8–3 218 m; annual rainfall: 704 ± 148, 336–1 203 mm; annual temperature (max. + min. /2): 18.3 ± 2.4, 4.8–25.1°C (N=299).

Habitat: In Gauteng bushveld: strong bias to sandy clay loam (2 759) compared to deep sand (638) primarily in open vegetation: grassland (2 197), open woodland (1 171), shaded thickets (29); supported in uMkhuze Game Reserve: sand (0.1), sand over clay (0.8), sandy clay loam (6.5), clay (1.0); also supported by DBRU collection records from sand (40), sandy loam (52), sandy clay loam (53), clay (5) in grassland/pasture (85), open shrub/woodland (44), forest/thicket (3).

Food types: At Phalaborwa: attracted more abundantly to dung of cattle (287) than that of elephant (90) or pig (93); supported in Gauteng bushveld: cattle (48), horse (24), pig (9), carrion (0); DBRU collection records from dung of cattle (167), buffalo (3), wildebeest (1), impala (1), elephant (3), horse (2), human (2).

Temporal activity: Diurnal flight activity; in Gauteng: midday peak (12:00–14:00) in Nov. to Feb., mid-afternoon peak (14:00–16:00) in Mar.; active mainly throughout summer rains (Oct. to Apr.), declining into dry season (May); low numbers active at end of dry season (Aug., Sept.); at Phalaborwa: greater abundance on a warm sunny day soon after heavy rainfall (322) than on a hot sunny (124) or a warm cloudy day following light rainfall (3); after colonising and shredding cattle pads, make and roll ball only on the following day.

Ecoregions Zimbabwe: Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome); Sub-Escarpment Grassland (Gs) (Grassland Biome); Albany Thicket (AT) and Indian Ocean Coastal Belt (CB) biomes; marginal in E Eastern Kalahari Bushveld (SVkb) (Savanna Biome) plus N Mesic Highveld Grassland (Gm), Dry Highveld Grassland (Gh) (Grassland Biome).

Assessment rationale: EOO = 720 705 km^2 (? underestimated); widespread across both reserves and farmland where it shows a bias to the dung of pad-dropping ruminant herbivores in open vegetation including farm pastures; thus little threatened in areas dominated by grazing of farm livestock; assessed as Least Concern (LC).

Conservation measures: None recommended; protected in Kruger National Park, uMkhuze Game Reserve (South Africa).

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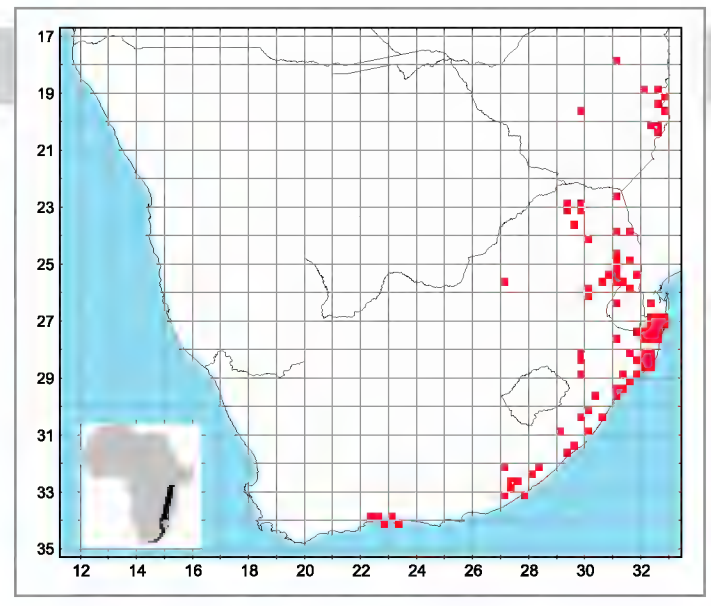
Neosisyphus spinipes

(Thunberg, 1818) (but see Taxonomy)

= *Sisyphus atratus* Klug, 1855
= *Sisyphus appendiculatus* Boheman, 1857
= *Sisyphus hessei* Gory, 1833
= *Sisyphus quadricollis* Gory, 1833, *sensu* Péringuey, 1901

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: As *Ateuchus spinipes*: 'majorem horum partem in capite bonae spei collegi' [amongst material mostly collected in the Cape of Good Hope, South Africa]; *S. atratus*: 'Tette' [Tete, central Mozambique]; *S. appendiculatus*: 'Caffraria tota' [inexact; ?all SE South Africa], lectotype: 'Caffraria'; *S. hessei*: 'Cap B.-Esp.' [Cape of Good Hope, South Africa], lectotype: Not stated; *S. quadricollis* Gory *sensu* Péringuey: 'Cape Colony (Transkei, Port Elizabeth, Stockenstroom, Graham's Town, Somerset East) Natal (Durban), Mozambique (Lourenço-Marquez and Beira, Sena...)' [South Africa: Eastern Cape, KwaZulu-Natal; Mozambique].

Taxonomy: Accepted species (but recent status change: genus *Sisyphus* Latreille, 1807; subgenus *Neosisyphus* Müller, 1942); limited sexual dimorphism (legs).

Distribution: Moist, warm savanna and grasslands on the E seaboard from S to NE Africa: South Africa, Zimbabwe, Mozambique, Zambia, Democratic Republic of the Congo (DRC), Rwanda, Burundi, Uganda, Tanzania, Kenya, Ethiopia; also reported from Botswana; citation from Senegal presumed an error.

Locality data (mean ± SD, range): Altitude: 484 ± 485, 0–1 706 m; annual rainfall: 823 ± 200, 462–1 659 mm; annual temperature (max. + min. /2): 20.2 ± 2.3, 14.4–25.2°C (N=126).

Habitat: No adequate quantitative data; soil generalist in uMkhuze Game Reserve: sand (2.8), duplex soil (sand over clay) (4.3), sandy clay loam (4.6), clay (2.2); supported by DBRU collection records: sand (23), sandy loam (7), sandy clay loam (21), clay (6) in grassland/pasture (37), open shrub/woodland (18), forest/thickets (4).

Food types: No quantitative assessment; DBRU collection records from dung of cattle (60), wildebeest (3), elephant (3), rhinoceros (1), horse (1), human (1), mix of human and cattle or buffalo (3).

Temporal activity: Diurnal flight activity during the summer rainy season (Oct.–Apr.) and also cooler, drier months at the warmer coastline (Aug., Sept., May).

Ecoregions Zimbabwe, Mozambique: Southern Miombo Woodlands (AT0719), Maputaland Coastal Forest Mosaic (AT0119).

Bioregions South Africa: Moist parts of Lowveld (SVl) (Savanna Biome), Indian Ocean Coastal Belt Biome (CB); also moist, warm E margins of Central Bushveld (SVcb) (Savanna Biome), Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs) (Grassland Biome); outlier in transformed pasture habitats in Eastern Cape (Fynbos Biome).

Assessment rationale: EOO = 1 156 170 km^2 (underestimated; NE African range omitted); apparently a soil generalist centred on warm moist grassland and savanna habitats, probably due to habit of cementing brood balls to grass stalks, or other vegetation, rather than burying them in soil; not susceptible to woodland clearance due to grassland habitat bias; also widespread; therefore assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; protected in Kruger National Park and Hluhluwe–iMfolozi Game Reserve.

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2 mm

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2 mm

Genus *Sisyphus* Latreille, 1807

(recent status change, three subgenera: *Sisyphus*, *Neosisyphus* Müller, 1942, and *Parasisyphus* Barbero, Palestrini & Zunino, 1991)

Type species and designation: *Sisyphus schaefferi* Linnaeus, 1758, by monotypy.
Synonyms: None.
Last review: All species reviewed by Haaf (1955); southern African species reviewed by Paschalidis (1974, unpublished); recent piecemeal revisions and addition of many new valid Afrotropical species (Endrödi 1973; Walter 1982; Cambefort 1984; Schafer & Fischer 1992, 2001; Montreuil 2014, 2015b, 2015c, 2017; Daniel et al. 2016); recent status change: *Sisyphus* divided into three subgenera (*Sisyphus*; *Neosisyphus* Müller, 1942; *Parasisyphus* Barbero, Palestrini & Zunino, 1991) by Daniel et al. (2020).

The long-established genus, *Sisyphus* Latreille, 1807, currently remains without a full recent revision. Subsequent to the earlier revision of the entire genus as two subgenera, *Neosisyphus* and *Sisyphus s. str.* (Haaf 1955), revisions were made to the southern African species by Paschalidis (1974). More recently, there has been piecemeal revision of some *Sisyphus* species groups and the addition of many new Afrotropical species (references listed above). Because of incomplete revision, southern African species listed here largely, though not entirely, follow Paschalidis (1974a) with the addition of modifications and new species added by Montreuil (2015b, 2015c) and Daniel et al. (2016). However, following the recent formal raising of *Neosisyphus* Müller, 1942, from subgeneric to generic level (Montreuil 2015a) , *Sisyphus* has now been redefined as three subgenera (Daniel et al. 2020) (*Sisyphus* Latreille, 1807; *Parasisyphus* Barbero, Palestrini & Zunino, 1991; *Neosisyphus* Müller, 1942). Although the old pre-2020 classification system is used, here, a note is included with group patterns and species accounts to indicate whether they belong to the subgenera *Sisyphus* or *Parasisyphus* under the new system.

At the end of 2017, *Sisyphus* comprised a total of 50 species with distributions throughout the Afrotropical (37), S Oriental (10) and S Palaearctic regions (1) with further species (2) isolated in central America at the N tip of the Neotropical region. A few new Oriental species have also been described since the revision of Haaf (1955) whereas further new Afrotropical species were added by Daniel et al. (2018) for which there are no species accounts. Species accounts have, however, been prepared for a total of 15 named species occurring in South Africa, Botswana and Namibia.

Group patterns in southern Africa: Group designations are based on relationships indicated by Paschalidis (1974) and Montreuil (2015b, 2015c, 2017). Five groups occur in southern Africa.

Group *costatus*: Four species centred on SE upland grasslands (2), SE savanna (1) or widespread in savanna with a distribution into the tropics (1) (recent status change: subgenus *Parasisyphus* Barbero, Palestrini & Zunino, 1991).

Group *impressipennis*: One savanna species with bias to shade distributed into the E tropics (recent status change: subgenus *Parasisyphus* Barbero, Palestrini & Zunino, 1991).

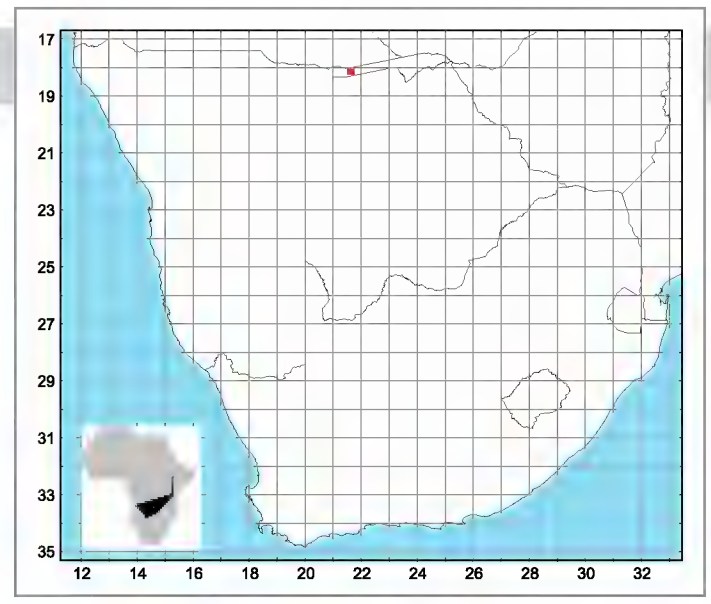
Group *muricatus*: Six species characterised by tufts of setae; three larger-bodied species centred on SE Highveld Grassland plus cooler S coast (1), SE coastal forest (1) or SE shady savanna plus NE escarpment forest (1); three smaller-bodied species centred on moist SE upland grassland and moist SE savanna (1), S coast (1) or N Namibia distributed into the E tropics (1, brachypterous) (recent status change: subgenus *Parasisyphus* Barbero, Palestrini & Zunino, 1991).

Group *ocellatus*: Two species found in shady situations in E savanna (1) or SE coastal forest (1) (recent status change: subgenus *Sisyphus* Lateille, 1807.

Group *seminulum*: Two species found in shady lowland savanna along the E seaboard of Africa (1) or in N Namibia and Angola (1) (recent status change: subgenus *Sisyphus* Lateille, 1807.

Sisyphus alveatus

Boucomont, 1935



No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Kenya Colony, Kibwezi, Wa-Kamba', lectotype: Afrique Orle anglaise, Kibwézi (Wa-Kamba) [Kibwezi, Kenya].

Taxonomy: Accepted species (recent status change: subgenus *Parasisyphus* Barbero, Palestrini & Zunino, 1991) in a group comprising macropterous and brachypterous taxa; in an unpublished revision of southern African *Sisyphus* (Paschalidis 1974a), *S. alveatus* from South Africa is cited in error for a species recently described as *Sisyphus manni* Montreuil, 2015c; citations from Zimbabwe (as Rhodesia) (Paschalidis, 1974a) cannot be validated (material missing).

Distribution: Moist savanna of S central Africa to NE Africa: Namibia, Angola, Zambia, Mozambique, Tanzania, Kenya, Ethiopia; in Namibia, known only from Epupa Falls, which are bordered by riparian vegetation.

Locality data: Altitude: 910 m; annual rainfall: 541 mm; annual temperature (max. + min. /2): 22.6°C (N=1).

Habitat: No quantitative assessment; no data.

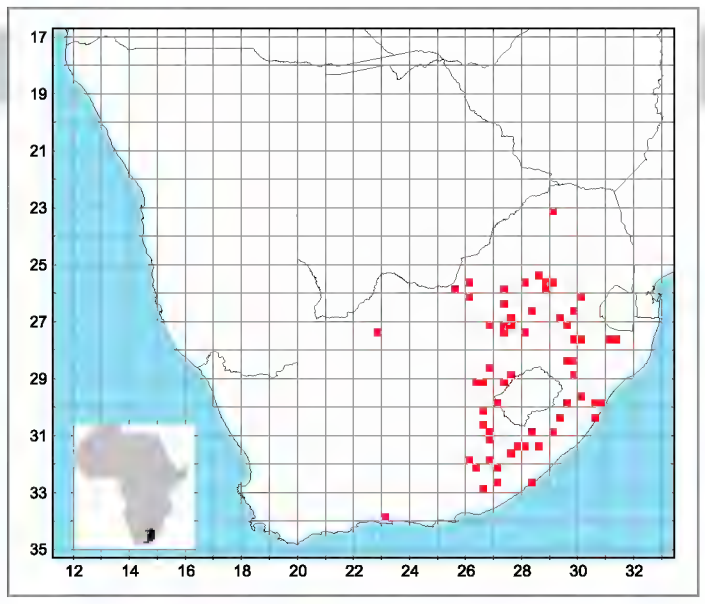
Food types: No quantitative assessment; no data.

Temporal activity: Brachypterous; diurnal activity during the summer rainy season (Nov.).

Ecoregions Namibia: Zambezian Baikiaea Woodlands (AT0726).

Assessment rationale: EOO = 1 801 180 km^2 (gross estimate); AOO presumably very much smaller than widespread EOO, but very poorly known ecologically; may be susceptible to habitat modification as a brachypterous species; in the absence of detailed data, assessed as Data Deficient (DD).

Conservation measures: To assess conservation status, a survey is required to determine if AOO is particularly restricted within the extensive EOO; quantitative data on ecological associations is also required from several localities across its wide range; protected in Mkomazi Game Reserve, Tanzania.



Sisyphus caffer

Boheman, 1857

No synonyms

Global: LC
Endemic: RSA (see IUCN Red List – LC)

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Caffraria tota, passim' [everywhere in all SE South Africa].
Taxonomy: Accepted species (recent status change: subgenus *Parasisyphus* Barbero, Palestrini & Zunino, 1991).
Distribution: Cool, moist grasslands of central to S Highveld and SSE coastal regions, South Africa with outlier occurrence in the N at higher altitude on the Blouberg.
Locality data (mean ± SD, range): Altitude: 1 260 ± 383, 43–1 782 m; annual rainfall: 674 ± 118, 339–948 mm; annual temperature (max. + min. /2): 16.5 ± 1.7, 12.9–20.0°C (N=71).
Habitat: On sandy loam in Ithala Game Reserve: recorded primarily in upland grassland (47, 1 330 m), few in mid-altitude grassland (1, 963 m), none in open shrub-woodland at lower altitude; on an altitudinal transect at latitude 29–30°S on the wet E escarpment: recorded in low numbers at 500 m (0.1 per trap) and 1 500 m (0.1), but not at higher altitudes (1 900–2 800 m); DBRU collection records primarily on finer-grained soils, sand (7), sandy loam (11), sandy clay loam (7), clay (3) almost exclusively in grassland/pasture (22) with one in shrubland.
Food types: In Ithala Game Reserve: primarily on pig (27) and cattle dung (19), few on horse dung (2); DBRU collection records exclusively from cattle dung (35).
Temporal activity: Diurnal flight activity, primarily during the summer rainy season (Oct. to May).
Bioregions South Africa: Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs), E Dry Highveld Grassland (Gh) (Grassland Biome); Indian Ocean Coastal Belt Biome (CB); S upland margins of Central Bushveld (SVcb) including high altitude outlier on Blouberg (Savanna Biome); marginal occurrence in four other bioregions.
Assessment rationale: EOO = 31 865 km^2 (main range minus N outlier on Blouberg); widespread and locally abundant on the South African Highveld in both pastures and natural grassland, mainly in cattle dung on farms, but also in reserves; therefore, assessed as Least Concern (LC).
Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, including effects of loss of natural grassland through pasture improvement or commercial forestry; protected in Ithala Game Reserve and Vernon Crookes Nature Reserve (KwaZulu-Natal, South Africa).

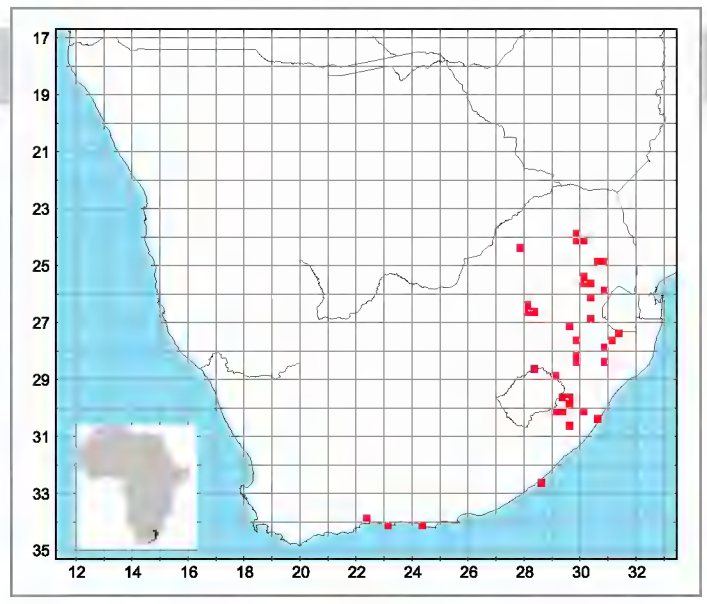
Sisyphus costatus

(Thunberg, 1818)

= *Sisyphus rugosus* Roth, 1851

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: As *Ateuchus costatus*: 'majorem horum partem in capite bonae spei collegi' [amongst material mostly collected in the Cape of Good Hope, South Africa]; *S. rugosus* Roth: 'Tigré in N. Abyssinien' [Tigray Province, N Ethiopia].

Taxonomy: Accepted species (recent status change: subgenus *Parasisyphus* Barbero, Palestrini & Zunino, 1991); as *S. costatus* is considered to be endemic to South Africa, the synonymy of *S. rugosus* Roth, 1851, is probably an error as it would represent a different Ethiopian species bearing a pre-occupied name.

Distribution: Only moist E Highveld and lowlands along the S coast of South Africa; reports from Zimbabwe, Mozambique, Tanzania, Kenya not supported by extensive DBRU collecting; also, further E and W African records (Burundi, Democratic Republic of the Congo (DRC), Ethiopia, Guinea, Côte d'Ivoire, Senegal) likely represent different species (see Taxonomy).

Locality data (mean ± SD, range): Altitude: 1 326 ± 541, 17–2 274 m; annual rainfall: 788 ± 134, 427–1 157 mm; annual temperature (max. + min. /2): 15.8 ± 2.0, 10.6–19.6°C (N=45).

Habitat: No adequate quantitative assessment; at Carolina: recorded in natural *Themeda* grassland (22) and fallow crop fields (31), but rare in improved Kikuyu pasture (2); DBRU collection records entirely from finer-grained soils: sandy loam (5), sandy clay loam (5), clay (2) in grassland/pasture (10).

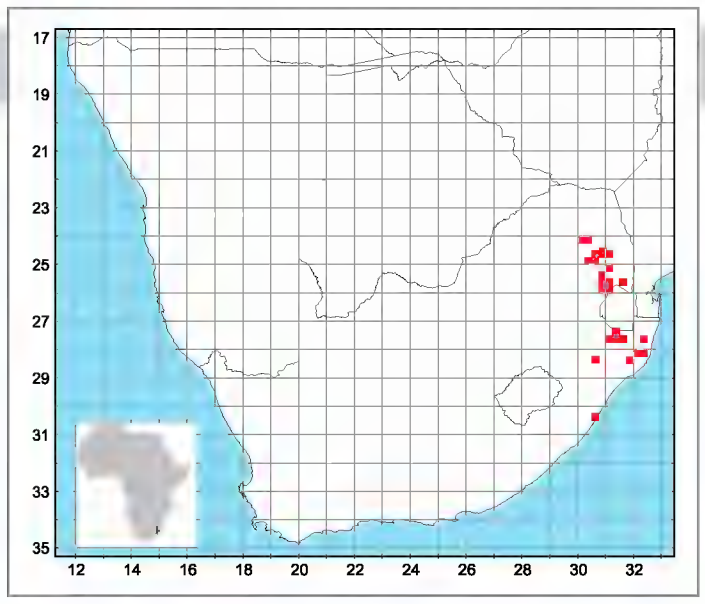
Food types: In Ithala Game Reserve: strong bias to pig dung (306) compared to horse (24) and cattle dung (57); DBRU collection records all from cattle dung (13).

Temporal activity: Diurnal flight activity during the summer rainy season (Oct. to Mar.).

Bioregions South Africa: Primarily, Mesic Highveld Grassland (Gm), Sub-Escarpment Grassland (Gs) (Grassland Biome); also Indian Ocean Coastal Belt Biome (CB) and pasture or crop fields in Eastern Fynbos-Renosterveld (F0 6).

Assessment rationale: EOO = 142 520 km^2; widespread with some tolerance of habitat transformation, which is often extensive across its main Grassland Biome range (6–69%, Gm; 3–50%, Gs); marginal presence in Fynbos Biome may be a response to habitat transformation; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by quantitative data on soil and vegetation associations; protected in Vernon Crookes and Suikerbosrand nature reserves; also Ithala Game Reserve, but largely localised to degraded open *Combretum* woodland at relatively low altitude.



Sisyphus fasciculatus

Boheman, 1857

No synonyms

Global: LC (see IUCN Red List – LC)
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Caffraria interiore rarius' [at wide intervals, SE South Africa].

Taxonomy: Accepted species (recent status change: subgenus *Parasisyphus* Barbero, Palestrini & Zunino, 1991).

Distribution: Localised in patches of lower-altitude forest and dense woodland; NE KwaZulu-Natal and inland along E escarpment to the NW of South Africa.

Locality data (mean ± SD, range): Altitude: 755 ± 487, 48–2 005 m; annual rainfall: 837 ± 78, 712–1 022 mm; annual temperature (max. + min. /2): 19.1 ± 2.2, 12.5–22.0°C (N=31).

Habitat: No adequate quantitative study; in uMkhuze Game Reserve: only on clay (1.2/trap), not sandy clay loam or sand; on finer-grained soils in Ithala Game Reserve: sampled to pig dung more abundantly in low-altitude shaded woodland (143, 758 m) than in mid-altitude forest (100, 1 077 m) and low-altitude degraded *Combretum* woodland (39, 884 m) or shrubland (32, 998 m), absent from lower (919 m) and higher altitude grassland (1 184 m); at Wolkberg: only in lower forest (16, 901 m) not higher forest (0, 1 355 m); on Mariepskop: only in forest at 900–1 000 m (21), not 1 500 m or above (0); poor DBRU collection records: sandy clay loam (2), clay (1) in forest (2) and grassland/pasture (2).

Food types: In Ithala Game Reserve: abundant on pig (214) and cattle dung (165), less so on horse (35); at Mariepskop and Wolkberg: pig dung (17/6), cattle dung (4/10); DBRU collection records from human/cattle dung mixture (2) and cattle dung (1).

Temporal activity: Diurnal flight activity, primarily during the summer rainy season (Oct. to Apr.).

Bioregions South Africa: Lower margins of Northern Mistbelt Forest patches (FOz 4), Scarp Forest patches (FOz 5), (Forest Biome) and dense woodland along the moist W edge of the Lowveld (SVl) (Savanna Biome) where it abuts onto the Grassland and Indian Ocean Coastal Belt Biomes.

Assessment rationale: EOO = 50 820 km^2; AOO would be much smaller due to possible finer-grained soil and observed shade association; thus, highly susceptible to clearance of dense woody vegetation over entire range; in forest patches (FOz 4, FOz 5), 20–25% is currently protected; although abundant in dense woodland of vulnerable lowland savanna units of Zululand, transformation is 22–26% (SVl 22, SVl 23) with only 4–11% conserved; however, currently assessed as Least Concern (LC) owing to protection in various reserves.

Conservation measures: Across the EOO, protection of forest and dense woodland patches would be essential for the conservation of this species; assessment of conservation status would be improved by further quantitative data on habitat associations; protected in Ithala, uMkhuze, Hluhluwe–iMfolozi game reserves plus Lekgalameetse, iSandlwana and Vernon Crookes nature reserves.

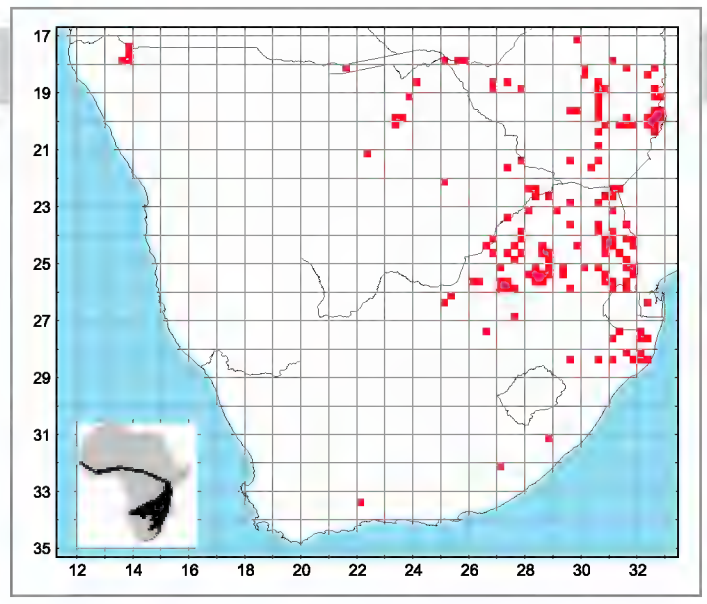
Sisyphus goryi

Harold, 1859

= *Sisyphus hirtus* Gory, 1833

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: *S. goryi*, *nom nov.* for *S. hirtus* Gory [pre-occupied name]: 'Sénégal' [Senegal].

Taxonomy: Accepted species (recent status change: subgenus *Parasisyphus* Barbero, Palestrini & Zunino, 1991), but may represent a species complex considering the geographical variation reported from across its widespread distribution.

Distribution: Moist savanna from S to E to W Africa; Senegal, Côte d'Ivoire, Nigeria, Kenya, Tanzania, Angola, Zimbabwe, Mozambique, Botswana, Namibia, South Africa; also reported from Gambia, Ethiopia.

Locality data (mean ± SD, range): Altitude: 906 ± 419, 5–1 850 m; annual rainfall: 666 ± 191, 246–1 415 mm; annual temperature (max. + min. /2): 20.1 ± 2.2, 13.4–25.2°C (N=214).

Habitat: In Gauteng bushveld: relatively generalist soil associations (sand: 1 091; sandy clay loam: 797) with very strong bias to open woodland (1 666) compared to grassland (130) and shaded thicket (92); DBRU collection records from sand (21), sandy loam (35), sandy clay loam (27), clay (5) in grassland/pasture (28), open shrub/woodland (45), thicket/forest (3), crop field (1).

Food types: In Gauteng bushveld: extreme bias to pig dung (46) with few on carrion (3); however, at Phalaborwa: equally strong bias to pig (3 041) and cattle dung (2 770) with many also attracted to elephant dung (584); DBRU collection records from dung of cattle (83), buffalo (4), impala (3), elephant (9), rhinoceros (1), zebra (1), donkey (4), horse (1), baboon (1), human (3).

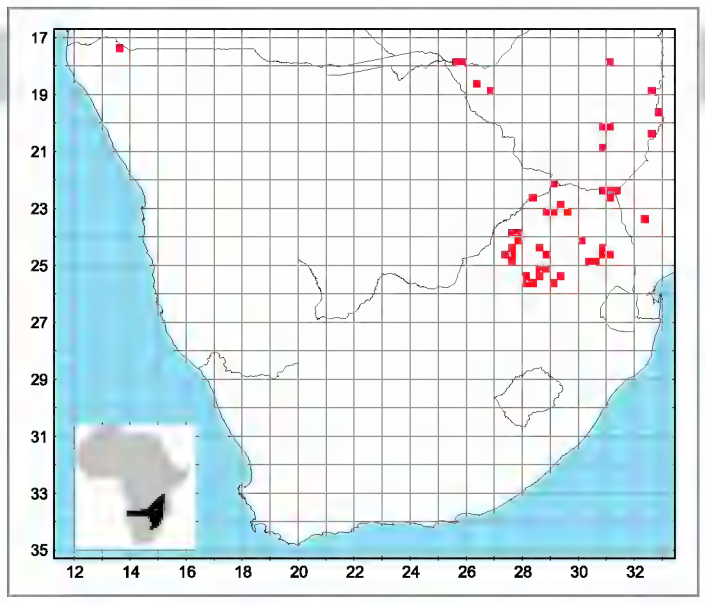
Temporal activity: Diurnal flight activity during the summer rainy season (Oct. to May); in Gauteng bushveld: late morning peak in flight activity (10:00–12:00, Nov. to Feb.) tailing off to late afternoon (12:00–16:00) moving to a midday peak in Mar. (12:00–14:00); seasonal peak primarily in early to mid-summer (Oct. to Jan.) tailing off steeply in late summer (Feb. to Apr.); at Phalaborwa: more active in warm sunshine after heavy rain (3 839) than in hot, sunny, but dry weather (1 904) or warm, but cloudy weather after light rain (554).

Ecoregions Namibia, Botswana, Zimbabwe, Mozambique: N Namibian Savanna Woodlands (AT1316), Kalahari Acacia-Baikiaea Woodlands (AT0709), Zambezian and Mopane Woodlands (AT0725), Southern African Bushveld (AT0717), Southern Miombo Woodland (AT0719); Maputaland Coastal Forest Mosaic (AT1119).

Bioregions South Africa: Central Bushveld (SVcb), Mopane (SVmp), Lowveld (SVl) (Savanna Biome); marginal in seven other bioregions.

Assessment rationale: EOO = 5 042 590 km² (gross estimate); widespread and locally abundant on various dung types; however, population density would be strongly reduced by clearance of woodland (habitat transformation: 0–58% (SVl); 2–49% (SVcb); 0–20% (SVmp)); nevertheless common with extremely wide range; assessed as Least Concern (LC).

Conservation measures: Further taxonomic study is required to determine if *S. goryi* comprises a single widespread species or a complex of species; protected in various national parks including: Kruger (South Africa), Manyara (Tanzania), Tsavo (Kenya).



Sisyphus impressipennis

van Lansberge, 1886

= *Sisyphus transvaalensis* Péringuey, 1908
= *Sisyphus callosipes* Arrow, 1909

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type localities: *S. impressipennis*: 'Humpata' [Angola]; *S. transvaalensis*: 'Transvaal (Zoutpansberg)' [Limpopo Province, South Africa]; *S. callosipes*: 'German East Africa: Massailand; British Central Africa: Nyasaland; Katanga, 150–200 miles west of Kambove; Mashonaland: Chirinda' [Tanzania, Malawi, Democratic Republic of the Congo (DRC), Zimbabwe].

Taxonomy: Accepted species (recent status change: subgenus *Parasisyphus* Barbero, Palestrini & Zunino, 1991); limited sexual dimorphism (legs).

Distribution: Localised in lowland forest and dense, shady woodland, savanna patches from E to S central and southern Africa: N South Africa, Botswana, Zimbabwe, Malawi, Mozambique, N Namibia, Angola, Tanzania; also reported from Democratic Republic of the Congo (DRC).

Locality data (mean ± SD, range): Altitude: 987 ± 443, 13–2 005 m; annual rainfall: 693 ± 227, 306–1 256 mm; annual temperature (max. + min. /2): 20.0 ± 2.8, 12.5–25.2°C (N=59).

Habitat: No adequate quantitative assessment; in dry savanna of Tswaing Nature Reserve: mainly in shaded thicket on crater rim (22), rare in pasture (1), absent from shrubland and open woodland; DBRU collection records from sand (1), sandy loam (4) in shrubland (1), open woodland (1), forest (18).

Food types: No quantitative assessment; DBRU collection records from various dung types: mixture of human and cattle or buffalo (14), baboon (1), elephant (4), rhinoceros (1), cattle (4), waterbuck (1).

Temporal activity: Diurnal flight activity during the summer rainy season (Nov. to Mar.).

Ecoregions Namibia, Zimbabwe: Dense shaded patches: N Namibian Savanna Woodlands (AT1316) (on Kunene River), Southern Miombo Woodlands (AT0719), Zambezian and Mopane Woodlands (AT0725), margins of two other ecoregions.

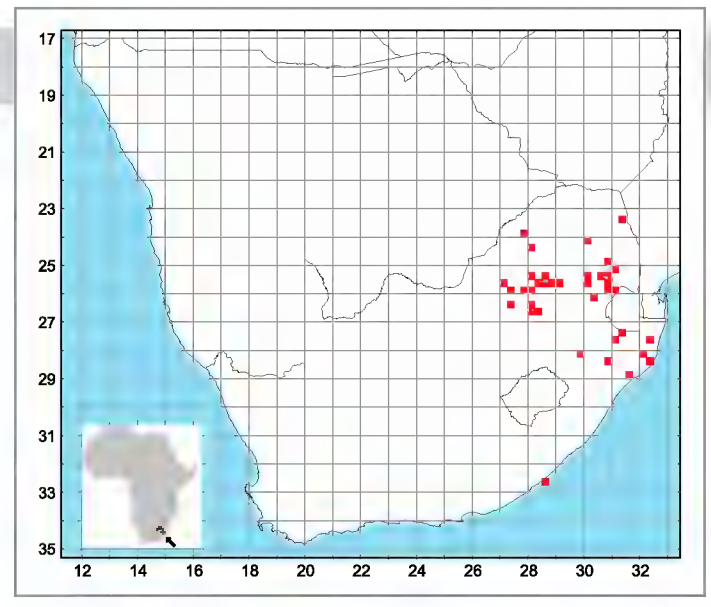
Bioregions South Africa: Central Bushveld (SVcb) (Savanna Biome).

Assessment rationale: EOO = 2 175 705 km^2; large range, but, as a shade specialist, AOO would be restricted to thicket and forest patches often associated with riverine, lacustrine or hill systems; would be susceptible to thinning as well as clearance of often drier forest and woodland; in South Africa transformation across range amounts to 2–49% (SVcb); assessed as Least Concern (LC) since widespread and widely protected.

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations; protected in various nature reserves (Tswaing, Leeuwfontein, Roodeplaat) as well as game reserves and national parks in South Africa (Kruger NP) and Zimbabwe (Lake Mutirikwe GR, Victoria Falls NP).

Sisyphus manni

Montreuil, 2015c



No synonyms

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'S. Africa: Limpopo, Kruger N.P.' [Kruger National Park, South Africa].

Taxonomy: Accepted macropterous species (recent status change: subgenus *Parasisyphus* Barbero, Palestrini & Zunino, 1991) in a species group comprising macropterous and brachypterous taxa; in an unpublished revision of southern African *Sisyphus* (Paschalidis 1974a), South African material cited in error as *Sisyphus alveatus* Gory, 1833 whereas cited Mozambique material is not *S. manni*; status of cited Zimbabwe material uncertain (material unavailable).

Distribution: Centred in warm, moist upland grassland or moist savanna around the N edge of the Highveld, along the Waterberg, and along the NE escarpment; also along the moist E coast in savanna or forest: South Africa; occurrence in Zimbabwe uncertain; occurrence in Mozambique not supported.

Locality data (mean ± SD, range): Altitude: 1 126 ± 509, 3–1 862 m; annual rainfall: 749 ± 118, 476–1 022 mm; annual temperature (max. + min. /2): 18.0 ± 2.3, 13.5–23.1°C (N=45).

Habitat: Data inconclusive; in Gauteng bushveld: recorded only on sandy clay loam (27), not deep sand (0) in grassland (12) and open woodland (15), not shaded thickets (0); in Leeuwfontein Nature Reserve: recorded in open woodland on both sand (13) and stony sandy loam (20); at Carolina: recorded primarily in natural *Themeda* grassland (337); much less common in fallow crop fields (37), rare in improved Kikuyu pasture (1); limited DBRU collection records from sandy loam (2), sandy clay loam (1) in pasture/grassland (3).

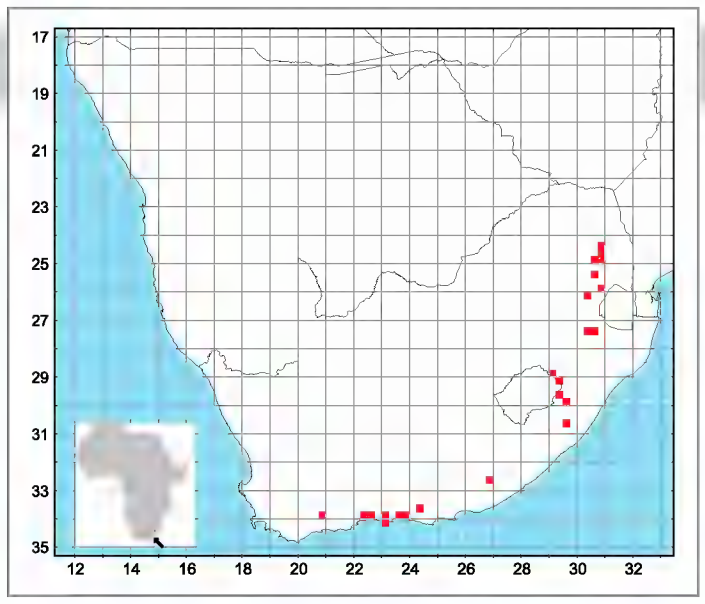
Food types: No quantitative assessment; limited DBRU collection records from dung of cattle (3).

Temporal activity: Macropterous; diurnal flight activity during the summer rainy season (Oct. to Mar.); on the Gauteng bushveld primarily active in early (Oct. to Dec.) and late summer (Mar.).

Bioregions South Africa: Largely centred along the moist N and E upland edges of the Grassland (Mesic Highveld Grassland) (Gm); Sub-Escarpment Grassland (Gs)) and Savanna Biomes (Central Bushveld (SVcb); Lowveld (SVl); also Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 124 410 km^2 (possibly underestimated); apparently susceptible to disturbance of natural vegetation through pasture improvement and cultivation; South African distribution coincides with often highly transformed vegetation units (e.g. 6–69%, N Gm, N Gs; 15–58%, S SVcb, S SVl); however, widespread and protected in various reserves; assessed as Least Concern (LC).

Conservation measures: Assessment of conservation status would be improved by further distributional and quantitative ecological data, particularly as soil associations seem to vary geographically; protected in Suikerbosrand, Abe Bailey and Leeuwfontein nature reserves as well as Hluhluwe–iMfolozi Game Reserve.



Sisyphus muricatus

(Olivier, 1789)

No synonyms

Global: LC
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: As *Scarabaeus muricatus*: 'l'Amérique méridionale' [Central America is undoubtedly an erroneous type locality for this South African endemic].

Taxonomy: Accepted species (recent status change: subgenus *Parasisyphus* Barbero, Palestrini & Zunino, 1991).

Distribution: South Africa; in summer rainfall region: found in a narrow band of cool, wet, montane conditions along E escarpment edge (average altitude: 1 556 m); in bimodal rainfall region of Eastern Cape: found on S coastal belt (262 m).

Locality data (mean ± SD, range): Altitude: 1 094 ± 735, 16–2 274 m; annual rainfall: 709 ± 228, 360–1 157 mm; annual temperature (max. + min. /2): 15.5 ± 2.4, 10.6–21.8°C (N=28).

Habitat: No adequate quantitative assessment; on a 500–2 800 m KwaZulu-Natal gradsect (29–30°S): rare in natural grassland on sandy clay loam at 1 500 m (0.2/trap), abundant at 1 900 m (28.7); at Carolina: recorded on sandy clay loam in natural grassland as a rarity (2), absent from improved Kikuyu pasture (Kikuyu) and fallow crop fields; recorded in forest areas but, currently, few records from forest; a single DBRU collection record from pasture on clay.

Food types: No quantitative assessment; a few DBRU collection records from cattle dung (3).

Temporal activity: Diurnal flight activity coinciding with summer (in the N) or spring/autumn rainfall peaks (in the S) (Sept. to Apr.).

Bioregions South Africa: In the N and E: moist E montane vegetation units, Mesic Highveld Grassland (Gm), Drakensberg Grassland (Gd), also Sub-Escarpment Grassland (Gs) (Grassland Biome); in the S: E vegetation units, Sandstone Fynbos (FFs), Shale Fynbos (FFh) (Fynbos Biome).

Assessment rationale: EOO = 24 500 km^2; extensive range in the N coincides with E edge of Grassland Biome, but unclear if it is a grassland specialist; thus, unknown if Eastern Cape range represents range expansion into pastures resulting from clearance of woody vegetation; range often coincides with vulnerable or endangered vegetation units resulting from tree plantations, cultivation and urbanisation (Gd 3–16%; montane Gm 23–52%, Gs 10–25%; Garden Route FFs 28–33%, FFh 50%); negative influence of pasture improvement and transformation possible, but poorly supported; currently assessed as Least Concern (LC) owing to widespread range.

Conservation measures: Assessment of conservation status would be improved by quantitative data on ecological associations, including possible effects of pasture improvement and habitat transformation; protected within the extensive uKhahlamba Drakensberg Park (World Heritage Site) along the E and NE Lesotho border.

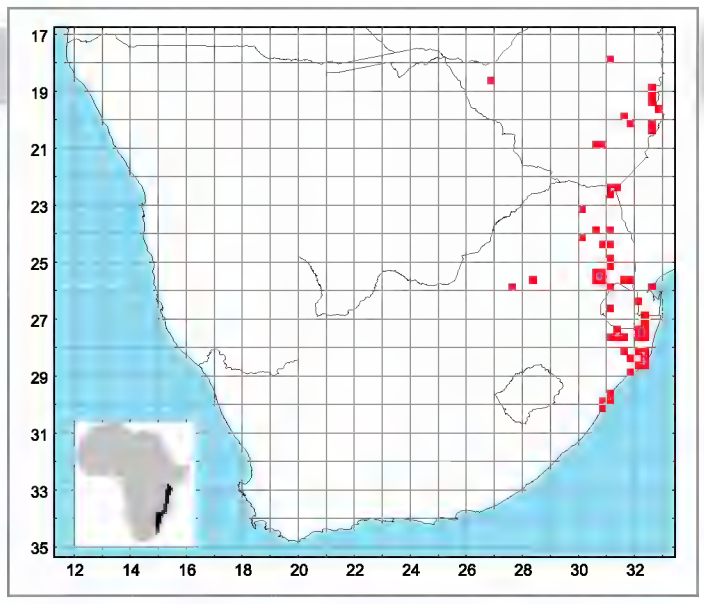
Sisyphus nanniscus

Péringuey, 1901

= *Sisyphus ocellatus* Reiche subsp. *nanniscus* Péringuey, 1901, *sensu* Haaf, 1955

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J



Type locality: 'Natal (Durban)' [KwaZulu-Natal, South Africa].

Taxonomy: Recently removed from published synonymy with *Sisyphus costatus* Thunberg, 1818, and *Sisyphus seminulum* Gerstaecker, 1871, to be re-established as a valid species (Montreuil 2016) (recent status change: subgenus *Sisyphus* Latreille, 1807); synonym (Haaf 1955) represents a misidentification of the species as a subspecies of *S. ocellatus* Reiche, 1847.

Distribution: Widespread across hot, woodland savanna from S to E Africa: South Africa, Botswana, Zimbabwe, Zambia, Malawi, Mozambique, Tanzania, Kenya.

Locality data (mean ± SD, range): Altitude: 523 ± 479, 0–1 613 m; annual rainfall: 811 ± 227, 383–2 097 mm; annual temperature (max. + min. /2): 20.7 ± 1.9, 13.8–25.2°C (N=74).

Habitat: In uMkhuze Game Reserve: relative soil generalist with slight bias to finer-grained soils, sand (36.8/trap), duplex soil (sand over clay) (45.5), sandy clay loam (57.0), clay (73.4) with 97% (2 255 out of 2 325) sampled under shade; in Hluhluwe Game Reserve: recorded in long grass on cloudy days; DBRU collection records from sand (15), sandy loam (10), sandy clay loam (5), clay (1) in forest/thicket (10), woodland (10), open shrub/woodland (8), grassland/pasture (4).

Food types: In Ithala Game Reserve: bias to dung of pig (2 902) and cattle (1 300) compared to horse (144); DBRU collection records from various dung types: human (1), baboon (1), human/cattle mix (6), elephant (1), rhinoceros (3), zebra (1), horse (1), warthog (1), cattle (20), buffalo (2), wildebeest (2), waterbuck (1), impala (1).

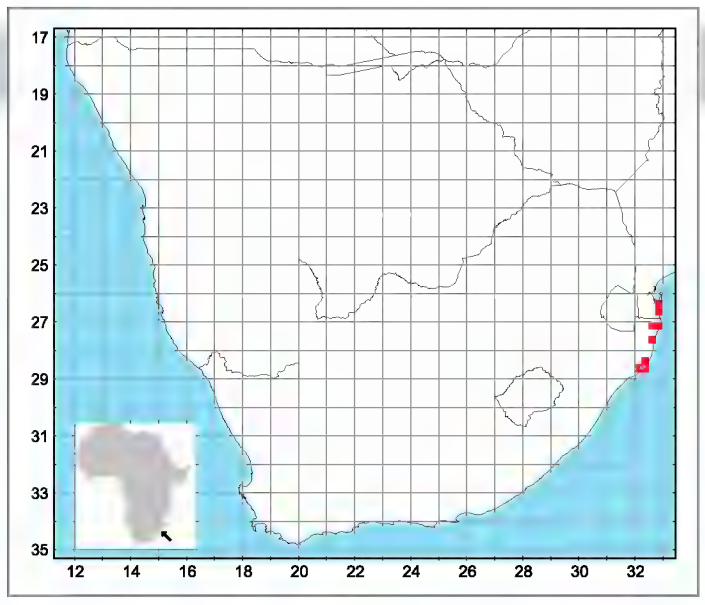
Temporal activity: Diurnal flight activity throughout much of the year due to warm lowland range, especially at the coast (Aug. to May).

Ecoregions Zimbabwe, Mozambique: Maputaland Coastal Forest Mosaic (AT0119), edge of the dry lowland Zambezian and Mopane Woodlands (AT0725) where it abuts onto moister, higher altitude ecoregions, particularly Southern Miombo Woodlands (AT0719).

Bioregions South Africa: Centred on Lowveld (SVl) (Savanna Biome), Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 919 450 km^2 (gross estimate); would be threatened by clearance of dense woodland and forest due to shade specialisation; in South Africa: transformation in main range (SVl) varies from 0 to 58%; however, widespread along E seaboard of Africa in hot, shaded, savanna vegetation; therefore, assessed as Least Concern (LC).

Conservation measures: None recommended; protected in Ithala, uMkhuze and Hluhluwe–iMfolozi game reserves as well as moister, densely wooded parts of the Kruger National Park (South Africa); also Meru Game Reserve (Kenya).



Sisyphus neobornemisszanus

Daniel & Davis, 2016

= *Sisyphus bornemisszanus* Endrödi, 1983 (*pars*)

Global: NT

J	A	S	O	N	D	J	F	M	A	M	J

Typelocalities: *S. neobornemisszanus*: 'Zululand, St. Lucia, 28.22S–32.25E'; *S. bornemisszanus*: 'Zululand, St. Lucia, 28.22S–32.25E' [KwaZulu-Natal, South Africa].

Taxonomy: Recently re-described as *S. neobornemisszanus* since *S. bornemisszanus* was represented by a type series comprising two different species; the holotype and some paratypes were synonymous with *Sisyphus sordidus* Boheman, 1857; only the allotype and remaining paratypes represented the species re-described as *S. neobornemiszanus* (recent status change: subgenus *Parasisyphus* Barbero, Palestrini & Zunino, 1991).

Distribution: Coastal-fringing dune forest in the Maputaland Centre of Endemism and further N along the Mozambique coast; South Africa, Mozambique.

Locality data (mean ± SD, range): Altitude: 8 ± 18, 0–64 m; annual rainfall: 844 ± 103, 738–1 006 mm; annual temperature (max. + min. /2): 22.3 ± 0.5, 22.7–23.6°C (N=22).

Habitat: On deep sand in Maputo Special Reserve: primarily in cooler coastal-fringing dune forest (34.8/trap) rather than warmer inland sand forest patches (large: 0.4, medium: 3.6, small: 1.9), absent from grassland patches (0); across a deep sand, post-mining chronosequence at Richards Bay: fewer in deep shade of early succession woodland (7) and natural dune forest (3) than in less-shaded later succession open understorey woodland (75); limited DBRU collection records in dune forest (5).

Food types: No quantitative assessment; sampled to pig dung.

Temporal activity: Diurnal flight activity during most of the year due to warm coastal range (Aug. to May).

Ecoregions Mozambique: Maputaland Coastal Forest Mosaic (AT0119); Southern Zanzibar-Inhambane Coastal Forest Mosaic (AT0128) (not shown on map).

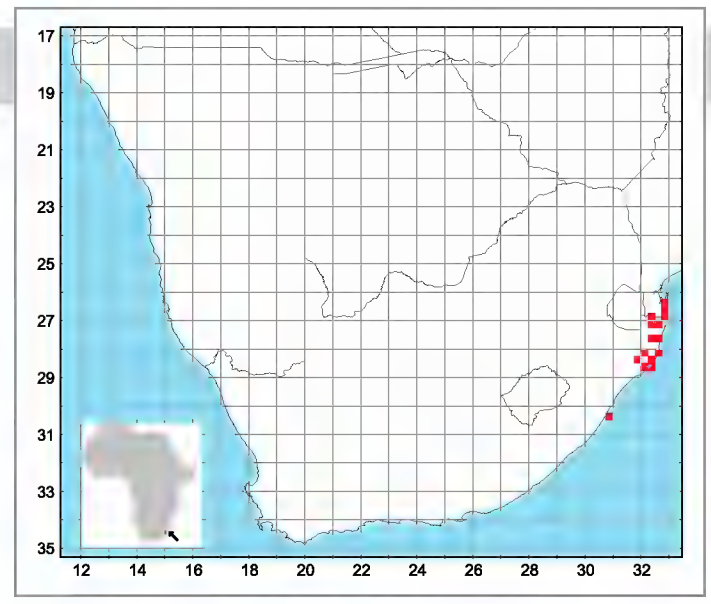
Bioregions South Africa: N Indian Ocean Coastal Belt Biome (CB).

Assessment rationale: EOO = 4 500 km^2; AOO smaller, restricted to dense woodland and forest patches; occurs along a coastline that has, in places, been transformed by mining; although it shows a larger range than the Maputaland endemic, *Scarabaeus bornemisszai* zur Strassen, which has been assessed as Near Threatened (NT), it is also assessed as NT owing to threats of coastal development; it would even qualify for an IUCN threat category approaching Vulnerable (VU) on the basis of small range and vegetation specialisation.

Conservation measures: Although quantitative data on soil and dung type associations would improve the assessment, conservation would clearly be dependent on the presence of regenerating woodland and/or protection of dune forest fringing the coast of NE KwaZulu-Natal (South Africa) and SE Mozambique; currently protected in iSimangaliso Wetland Park (World Heritage Site) (South Africa) and Maputo Special Reserve (Mozambique).

Sisyphus oralensis

Daniel & Davis, 2016



No synonyms

Global: LC

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'KZN, Richard's Bay' [Richards Bay, KwaZulu-Natal, South Africa].

Taxonomy: Accepted species (recent status change: subgenus *Sisyphus* Latreille, 1807) referenced as *Sisyphus* sp. y in the unpublished taxonomic revision of Paschalidis (1974a) and various ecological papers on the dung fauna of coastal NE KwaZulu-Natal.

Distribution: Moist to wet forest and shaded thicket on deep sands bordering SE African coast: NE South Africa, SE Mozambique.

Locality data (mean ± SD, range): Altitude: 28 ± 56, 0–273 m; annual rainfall: 853 ± 112, 634–1 010 mm; annual temperature (max. + min. /2): 22.0 ± 0.6, 20.0–23.3°C (N=32).

Habitat: Across a post-mining, rehabiltation gradient on coastal dunes at Richards Bay: grassland (0.00), early woodland (0.13), older woodland (2.46), natural dune forest (2.12); on deep sand in Maputo Special Reserve: absent from grassland (0), but present in all forest categories: large sand forest patches (12.7), medium-sized patches (21.2), small patches (11.1), cooler coastal dune forest (5.0); DBRU collection records exclusively from forest (9) or *Eucalyptus* plantation (1).

Food types: No quantitative assessment; DBRU collection records from dung of cattle (3) and human/cattle dung mix (1).

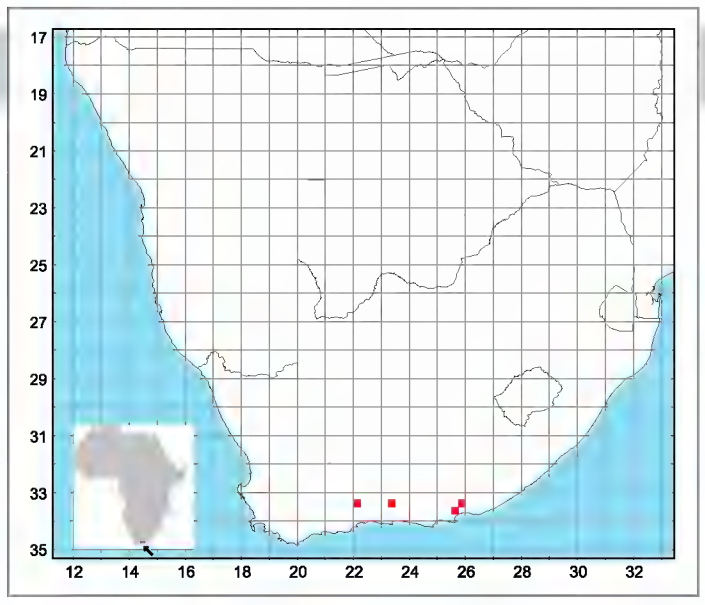
Temporal activity: Diurnal flight activity; recorded both during the summer rainy season (Oct. to Feb.) and the dry season (May to Aug.).

Ecoregions Mozambique: Maputaland Coastal Forest Mosaic (AT0119).

Bioregions South Africa: N Indian Ocean Coastal Belt Biome (CB); SE Lowveld (SVl) (Savanna Biome).

Assessment rationale: EOO = 18 105 km^2; although sand is widespread along the SE coastline, AOO would be much smaller due to specialised association with vegetation offering shade; quantitative data show that clearance of forest and thicket is detrimental to population density; however, *S. oralensis* is currently assessed as Least Concern (LC) by virtue of large EOO and occurrence at various localities.

Conservation measures: Assessment of conservation status would be improved by further quantitative data on ecological associations and further information on effects of the clearance of forest and dense woodland; protected in Maputo Elephant Reserve (Mozambique), Tembe Elephant Reserve and iSimangaliso Wetland Park (World Heritage Site) (South Africa).



Sisyphus perissinottoi

Montreuil, 2015c

No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'RSA, EC, Amsterdamhoek (Port Elizabeth)' [Eastern Cape, South Africa].

Taxonomy: Accepted species (recent status change: subgenus *Parasisyphus* Barbero, Palestrini & Zunino, 1991) in a species group comprising macropterous and brachypterous taxa.

Distribution: Centred on drier areas, E bimodal rainfall region, Eastern Cape, South Africa.

Locality data (mean ± SD, range): Altitude: 608 ± 494, 123–1 100 m; annual rainfall: 353 ± 88, 246–426 mm; annual temperature (max. + min. /2): 16.4 ± 1.8, 14.8–18.0°C (N=4).

Habitat: No quantitative assessment; not known.

Food types: No quantitative assessment; not known.

Temporal activity: Macropterous; diurnal flight activity; currently recorded only during the autumn peak of the bimodal rainfall spring/autumn rainy season (Feb.).

Bioregions South Africa: Albany Thicket Biome (AT), Rainshadow Valley Karoo (SKv) (Succulent Karoo Biome).

Assessment rationale: EOO = 9 685 km^2 (underestimated); only recently recognised as a valid species, but known by few localities with no associated ecological data; the low number of known localities (<5) within a small EOO would qualify for an IUCN threat category of Vulnerable (VU), but this pattern is considered to represent a collection artefact; therefore, currently, assessed as Data Deficient (DD).

Conservation measures: Assessment of conservation status will only be possible after a quantitative survey has been conducted in the bimodal rainfall region of the Eastern Cape to determine the full EOO, AOO and ecological associations; protected in Addo Elephant National Park.

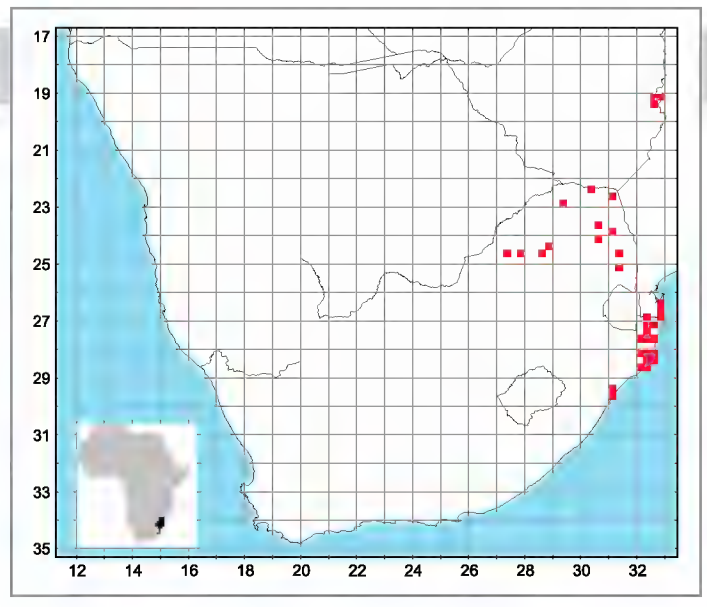
Sisyphus sordidus

Boheman, 1857

= *Sisyphus natalensis* Balthasar, 1968
= *Sisyphus bornemisszanus* Endrödi, 1983 (*pars*)

Global: LC (See IUCN Red List – LC as *S. natalensis*)

J	A	S	O	N	D	J	F	M	A	M	J



Type localities: *S. sordidus*: 'Caffraria interiore' [inexact, may be interior of SE Africa]; *S. natalensis*: 'Süd-Afrika, Nord-Natal. Umgebung von Santa Lucia Lake'; *S. bornemisszanus* (*pars*): 'Zululand, St. Lucia, 28.22S–32.25E' [both, environs of Lake St Lucia, KwaZulu-Natal, South Africa].

Taxonomy: Accepted species (recent status change: subgenus *Parasisyphus* Barbero, Palestrini & Zunino, 1991); as regards the synonyms, only part of the type series of *S. bornemisszanus* (holotype and five paratypes) is synonymous with *S. natalensis* (Daniel et al. 2016); the allotype and five other paratypes of *S. bornemisszanus* have been re-described as *S. neobornemisszanus* Daniel & Davis, 2016 (see species account).

Distribution: Primarily, moist lowland savanna, particularly on the Mozambique Coastal Plain, but also, along the Soutpansberg and Waterberg: South Africa, Zimbabwe, Mozambique.

Locality data (mean ± SD, range): Altitude: 225 ± 341, 0–1 148 m; annual rainfall: 803 ± 191, 362–1 254 mm; annual temperature (max. + min. /2): 22.0 ± 1.3, 18.8–25.2°C (N=59).

Habitat: In uMkhuze Game Reserve: extreme bias to deep sand (136.8) compared to sand over clay (2.3), sandy clay loam (0.0) and clay (0.1); across a vegetation recovery gradient at Richards Bay: extreme bias to grassland (706) compared to young woodland (4), older woodland (1) and natural dune forest (0); partly supported by DBRU collection records from sand (12), sandy loam (2) in grassland (15), open shrub/woodland (7), forest/thicket (7).

Food types: No quantitative assessment; DBRU collection records from various dung types including cattle (7), impala (1), horse (2), elephant (1), rhinoceros (2), human (3), human/cattle or buffalo mix (4).

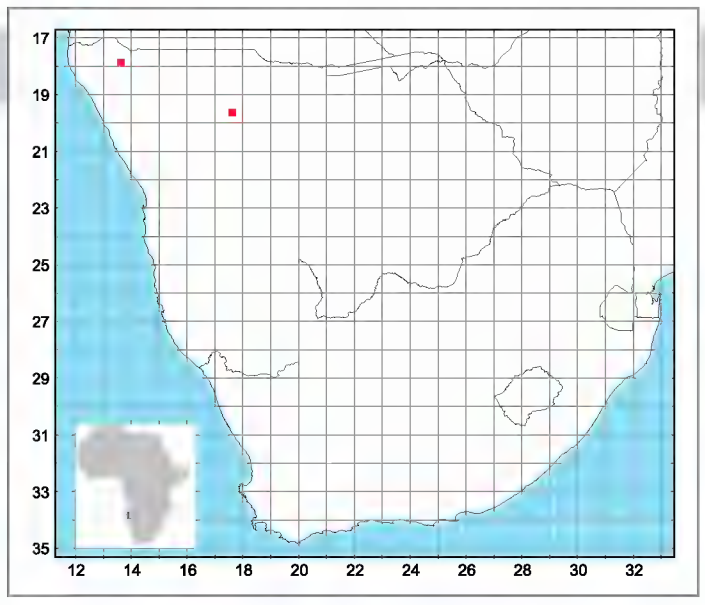
Temporal activity: Diurnal flight activity, primarily during the summer rainy season (Oct. to May).

Ecoregions Zimbabwe, Mozambique: E Southern Miombo Woodlands (AT0719), Maputaland Coastal Forest Mosaic (AT0119).

Bioregions South Africa: Centred on Indian Ocean Coastal Belt Biome (CB), also, Lowveld (SVl) plus Waterberg in Central Bushveld (SVcb), marginal in Mopane (SVmp) (Savanna Biome),.

Assessment rationale: EOO = 326 650 km^2 (N extent of EOO probably underestimated); AOO presumably smaller according to distribution of sand and open vegetation; assessed as Least Concern (LC) owing to large range, widespread occurrence of sand along SE coast and association with open vegetation, which would suggest tolerance of habitat tranformation.

Conservation measures: Assessment of conservation status would be improved by quantitative data on dung type associations although apparently a dung type generalist; protected in uMkhuze Game Reserve and iSimangaliso Wetland Park (World Heritage Site) (South Africa), Gorongosa National Park and Maputo Special Reserve (Mozambique).



Sisyphus splendidus

Montreuil, 2015b

No synonyms

Global: DD

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'Namibie,...., Otavi mts, Farm Gauss' [NW Namibia].

Taxonomy: Accepted species (recent status change: subgenus *Sisyphus* Latreille, 1807).

Distribution: Limited locality data suggest a range in mostly dry savanna regions across mountains and plains: NW Namibia, SW Angola.

Locality data (mean ± SD, range): Altitude: 1 495 ± 370, 1 227–1 917 m; annual rainfall: 563 ± 174, 389–737 mm; annual temperature (max. + min. /2): 18.7 ± 1.4, 17.2–19.9°C (N=3).

Habitat: Not known.

Food types: Not known.

Temporal activity: Not known, but presumably diurnal flight activity like other sisyphines; recorded during the late summer rainy season (Dec., Feb.).

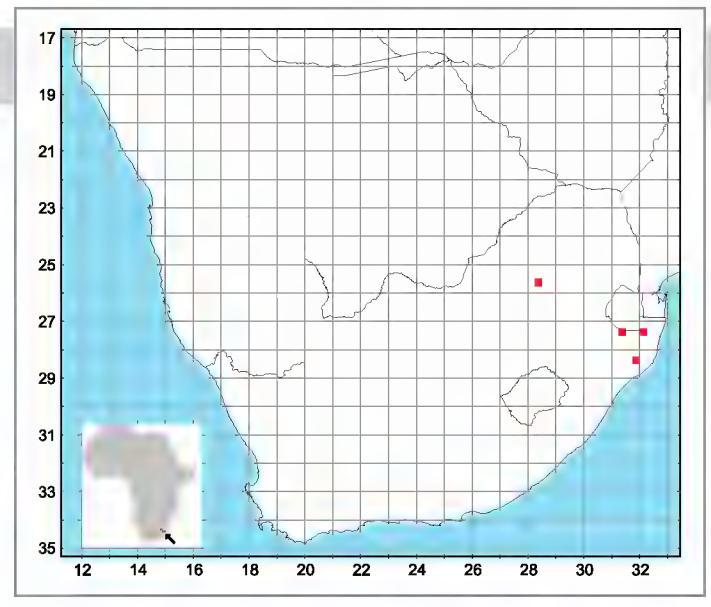
Ecoregions Namibia: NE Kalahari Xeric Savanna (AT1309), N Namibian Savanna Woodlands (AT1316).

Assessment rationale: EOO = 18 600 km^2 (estimated); only recently described as a new species; known by 18 individuals from only three localities, but recorded across a fairly wide range that has probably been underestimated; limited records probably a collecting artefact; if so, would deserve Least Concern (LC) status, but at present assessed as Data Deficient (DD).

Conservation measures: To assess conservation status, a quantitative survey of N Namibia and SW Angola is required to determine EOO, AOO and ecological associations; not currently known from any protected area.

Sisyphus umbraphilus

Daniel & Davis, 2016



No synonyms

Global: DD
Endemic: RSA

J	A	S	O	N	D	J	F	M	A	M	J

Type locality: 'KZN, Umfolozi' [iMfolozi Game Reserve, KwaZulu-Natal, South Africa].

Taxonomy: Accepted species (recent status change: subgenus *Sisyphus* Latreille, 1807) referenced as *Sisyphus* sp. x in the unpublished taxonomic revision of Paschalidis (1974a) and as *Sisyphus* sp. in ecological publications for Gauteng.

Distribution: A few scattered records in forest or shaded thickets in moist savanna regions: South Africa.

Locality data (mean ± SD, range): Altitude: 519 ± 487, 126–1 150 m; annual rainfall: 744 ± 124, 636–904 mm; annual temperature (max. + min. /2): 20.3 ± 1.4, 18.9–21.9°C (N=4).

Habitat: In Gauteng: recorded on deep sand (11) not sandy clay loam (0) and in shaded thickets (11) not open woodland (0) or grassland (0); in Ithala Game Reserve: recorded in moist, dense lowland woodland (10); one DBRU collection record from forest.

Food types: In Ithala Game Reserve: bias shown to omnivore dung (pig: 8) compared to herbivore dung, monogastric (horse: 0), ruminant (cattle: 2).

Temporal activity: Diurnal flight activity during the summer rainy season (Oct. to Jan.); in Gauteng: activity only recorded during the early rainy season (Nov. to Dec.).

Bioregions South Africa: Central Bushveld (SVcb), Lowveld (SVl) (Savanna Biome); marginal in one other bioregion.

Assessment rationale: EOO = 21 880 km^2 (undoubtedly underestimated); AOO would be much smaller as it is certainly a shade vegetation specialist; possibly also a soil and dung type specialist; assessed as Data Deficient (DD) owing to the limited number of records, which are probably a collecting artefact reflecting its specialised habits and low population density.

Conservation measures: To adequately assess conservation status, it is necessary to conduct a quantitative survey of thickets in savanna regions of South Africa; this survey should test soil and food associations more thoroughly and determine level of threat through clearance of dense woodland and forest; protected in Ithala and Hluhluwe-iMfolozi game reserves.

Poorly known species

This section comprises a number of poorly known, but currently valid species and their synonyms. They are mostly, wholly or partly described from South Africa, Botswana or Namibia. For the most part, they are known only from type material. They have, therefore, not yet been validly matched to available non-type reference specimens. Distributions are based on citations in Schoolmeesters (2017), but have not been critically assessed.

ATEUCHINI

Pedaria alternans

Waterhouse, 1890

No synonyms
Type locality: 'S. Africa' [?South Africa].
Distribution: South Africa, Ethiopia.
Notes: Not yet reliably matched to available southern African material.

Pedaria aspera

Péringuey, 1901

No synonyms
Type locality: 'Cape Colony (Barkly West)' [Northern Cape, South Africa].
Distribution: South Africa.
Notes: Not yet reliably matched to available South African material.

Pedaria conformis

Péringuey, 1901

= *Pedaria somalica* Balthasar, 1939a
Type localities: *P. conformis*: 'Transvaal (Klerksdorp, Potchefstroom), Natal (Durban)' [South Africa: North-West Province and KwaZulu-Natal]; *P. somalica*: 'Somalia, Obbia'.
Distribution: South Africa, Somalia.
Notes: Not yet reliably matched to available South African material; synonymy of *P. conformis* and *P. somalica* based on identical aedeagi possessed by male types (Josso & Prévost 2003).

COPRINI

Metacatharsius pusio

(Kolbe, 1908)

No synonyms
Type locality: As *Catharsius pusio*: 'Kalahari: Sekgoma-Khakea;....Khakea-Kang' [Botswana: Sekumo to Kang].
Distribution: Namibia, Botswana.
Notes: Not yet reliably matched to available Botswana material; however, see species account for *M. freyi* (Ferreira 1964b).

Metacatharsius rugosipennis

Frey, 1975

No synonyms
Type locality: 'Betchuanaland, Tsano' [?Tshane, Botswana].
Distribution: Botswana.
Notes: Not yet reliably matched to available Botswana material; however, see species account for *M. ferreirae* (Balthasar, 1965b).

Metacatharsius transvaalensis

Balthasar, 1968

No synonyms
Type locality: 'Süd-Afrika, Transvaal (Ost)' [?Mpumalanga Province, South Africa].
Distribution: N South Africa.
Notes: Not yet reliably matched to available southern African material.

ONTHOPHAGINI

Caccobius inconspicuus

(Fahraeus, 1857)

No synonyms
Type locality: As *Onthophagus inconspicuus*: 'in terra Natalensi' [KwaZulu-Natal, South Africa].
Distribution: South Africa, Malawi, Mozambique, Democratic Republic of the Congo (DRC).
Notes: Not matched to available southern African material.

Jossonthophagus asperriformis

Dierkens & Moretto, 2017

= *Onthophagus incertus* Péringuey, 1901
= *Onthophagus dubius* d'Orbigny, 1902
= *Onthophagus asperrimus* d'Orbigny, 1902
Type localities: *J. asperriformis*: 'Ovampoland (Omrramba)' [Omuramba, Ovamboland, Namibia] nom nov. for both *O. dubius* and *O. incertus* (pre-occupied names); *O. asperrimus*: 'Afrique orientale allemande' [Tanzania], lectotype: same locality.
Distribution: South Africa, Botswana, Namibia, Malawi, Zambia, Zimbabwe, Mozambique, Tanzania.
Notes: Formerly assigned to *Onthophagus* Group 14; revised by Dierkens et al. (2017).

Jossonthophagus dispar

(Péringuey, 1901)

No synonyms
Type locality: As *Onthophagus dispar*: 'Natal (Malvern)' [Queensburgh (Durban), KwaZulu-Natal, South Africa]; lectotype: same locality.
Distribution: Democratic Republic of the Congo (DRC), Zambia, Zimbabwe, Namibia, now validated; Angola, Tanzania, Mozambique require validation as well as the South African type locality.
Notes: Formerly assigned to *Onthophagus* Group 14; revised by Dierkens et al. (2017).

Onthophagus aschenborni

Frey, 1975b

No synonyms
Type locality: 'Nordtransvaal, Magoebaskloof' [Magoebaskloof, Limpopo Province, South Africa].
Distribution: South Africa.
Notes: Not yet reliably matched to available Group 2 South African material; cited as close to *O. modestus* Harold, 1862 (Frey 1975b).

Onthophagus asimilis

Péringuey, 1901

No synonyms
Type locality: 'Bechuanaland' [Botswana].
Distribution: Botswana, Namibia.
Notes: Not matched to available Group 16 southern African material.

Onthophagus aspericeps

d'Orbigny, 1908

No synonyms
Type locality: 'Sud-Ouest africain allemand: Okahandya' [Okahandja, Namibia].

Distribution: Namibia, South Africa.
Notes: Described from a single individual; not reliably matched to available Group 22 Namibian material; relationships to *O. convexus* d'Orbigny, 1908, need to be determined (see species account).

Onthophagus betschuanus

Frey, 1975

No synonyms
Type locality: 'S.-Afrika, Betschuanaland, Kukong' [Botswana].
Distribution: Botswana.
Notes: Not matched to available Botswana material in either Groups 2 or 22.

Onthophagus biconifer

d'Orbigny, 1905

No synonyms
Type locality: 'Transvaal' [N South Africa].
Distribution: South Africa, Democratic Republic of the Congo (DRC).
Notes: Not matched to available Group 2 southern African material.

Onthophagus burchelli

d'Orbigny, 1908

No synonyms
Type localities: 'Bechouana: Griquatown...Sud-Ouest africain allemand: Windhoek...Okahandja' [Griquatown, Northern Cape, South Africa; Namibia: Windhoek and Okahandja].
Distribution: South Africa (NOT Botswana), Namibia.
Notes: Not matched to available Group 24 southern African material; recently recognised as a synonym of *Onthophagus leucopygus* Harold, 1867 (P. Moretto, pers. comm.).

Onthophagus confertus

Péringuey, 1908

= *Onthophagus pusio* Péringuey, 1901
Type locality: *O. confertus nom nov.* for *O. pusio* Péringuey (pre-occupied name): 'Natal (Maritzburg)' [Pietermaritzburg, KwaZulu-Natal, South Africa].
Distribution: Zimbabwe, South Africa, Mozambique.
Notes: Not matched to available Group 19 South African material; needs to be compared with *O. pusio* Fahraeus, 1857.

Onthophagus coptorhinodes

Péringuey, 1901

No synonyms
Type locality: 'Natal (Estcourt)' [Estcourt, KwaZulu-Natal, South Africa].
Distribution: NE South Africa.
Notes: Not matched to available Group 3 South African material.

Onthophagus criniger

d'Orbigny, 1904

= *Onthophagus crinitus* d'Orbigny, 1902
See species account for *O. axillaris* Boheman, 1860.
Notes: Described from a single individual; not matched to available Group 16 Botswana material.

Onthophagus declivicollis

d'Orbigny, 1902

No synonyms
Type locality: 'Natal' [KwaZulu-Natal, South Africa].

Distribution: NE South Africa, Mozambique.
Notes: Not matched to available Group 9 South African material; needs to be compared with *O. asperulus* d'Orbigny, 1905, as a possible senior name.

Onthophagus dedecor

Wallengren, 1881

= *Onthophagus nigrescens* d'Orbigny, 1902
Type localities: *O. dedecor*: 'Transvaalia' [N South Africa], *O. nigrescens*: 'Zambèze....Transvaal' [inexact: southern Africa, N South Africa].
Distribution: Zimbabwe, South Africa.
Notes: Not matched to available Group 2 South African material; types need to be compared with *O. aeruginosus* Roth, 1851, and a close unnamed relative from the Waterberg, South Africa.

Onthophagus gnu

Frey, 1955

No synonyms
Type locality: 'Süd-West-Afrika Gobabis' [Gobabis, Namibia].
Distribution: Namibia.
Notes: Described from a single male individual, not matched to available Group 11 Namibian material; group assignment requires validation.

Onthophagus granulum

d'Orbigny, 1904

= *Onthophagus granum* d'Orbigny, 1902
Type locality: *O. granulum nom nov.* for *O. granum* (pre-occupied name): 'Mozambique...: Lourenço Marquez' [Maputo, Mozambique].
Distribution: N South Africa, Mozambique.
Notes: Matched to Group 2 South African material from Nylsvlei (Limpopo Province), but requires further validation by comparison with type.

Onthophagus guttatus

Boheman, 1860

No synonyms
Type locality: 'juxta lacum N'Gami' [near Lake Ngami, N Botswana].
Distribution: Botswana, Angola.
Notes: Not placed in a group by d'Orbigny (1913); not matched to available Botswana material.

Onthophagus importunus

Péringuey, 1901

No synonyms
Type locality: 'Ovampoland (Humbe)' [Ovamboland, Namibia].
Distribution: Namibia, Angola.
Notes: Not reliably matched to available Namibian Group 2 material.

Onthophagus insulsus

Péringuey, 1901

No synonyms
Type locality: 'Natal (Eshowe)' [Eshowe, KwaZulu-Natal, South Africa].
Distribution: South Africa
Notes: Not matched to available Group 7 South African material; needs to also be compared with *O. beiranus* Péringuey, 1908 (see species page), *O. interstitialis* Fahraeus, 1857, and two unnamed species from E forests of South Africa of similar body size.

Onthophagus lugens

Fahraeus, 1857

No synonyms
Type locality: 'juxta fluvium Gariep' [near Orange River, South Africa].
Distribution: South Africa, Zimbabwe.
Notes: Not matched to available Group 9 South African material; needs to be assessed as a possible synonym of *O. setosus* Fahraeus, 1857, as suggested by Péringuey (1901).

Onthophagus macrothorax

d'Orbigny, 1902

No synonyms
Type locality: 'Lac Ngami' [Lake Ngami, N Botswana].
Distribution: Botswana, Democratic Republic of the Congo (DRC).
Notes: Not matched to available Group 16 Botswana material.

Onthophagus marshalli

d'Orbigny, 1908

No synonyms
Type localities: 'Rhodésia: Salisbury...Bulawayo...Transvaal: Waterberg District…Sud-Ouest africain allemand: Otjosondu-Kub' [various localities: South Africa, Zimbabwe, Namibia].
Distribution: N South Africa, Zimbabwe, Namibia
Notes: Not matched to available Group 9 South African material; does not resemble any other species.

Onthophagus merus

Péringuey, 1901

No synonyms
Type localities: 'Cape Colony (Kimberley), Southern Rhodesia (Lesappi River)' [Northern Cape, South Africa; Zimbabwe].
Distribution: South Africa, Zimbabwe, Botswana.
Notes: Matched to available Group 31 South African material from Gauteng and to Zimbabwean material from Hwange National Park, but requires validation by comparison with type material.

Onthophagus minutulus

Harold, 1875

No synonyms
Type locality: 'Kuruman in Südafrika' [Kuruman, South Africa].
Distribution: South Africa, Botswana.
Notes: Not matched to available Group 3 southern African material.

Onthophagus modestus

Harold, 1862

= *Onthophagus pusillus* Fahraeus, 1857
Type locality: 'juxta fluvium Gariep' [near Orange River, South Africa].
Distribution: South Africa.
Notes: A *nom nov.* for pre-occupied name of *O. pusillus* Fabricius, 1801; not matched to available Group 2 South African material.

Onthophagus nanus

Harold, 1878

= *Onthophagus decipiens* Péringuey, 1901
Type localities: *O. nanus*: 'Ostafrika' [East Africa]; *O. decipiens*: 'Mossamedes, Natal (Malvern)' [Namibe, Angola; Queensburgh, KwaZulu-Natal, South Africa].
Distribution: Kenya, Malawi, Angola, Zimbabwe, Mozambique, South Africa, Namibia.
Notes: Not yet reliably matched to available Group 11 material from South Africa, Botswana and Namibia; synonymy of *O. decipiens* requires validation.

Onthophagus nudus

d'Orbigny, 1908

No synonyms
Type locality: 'Natal: Malvern' [Queensburgh, KwaZulu-Natal, South Africa].
Distribution: South Africa.
Notes: Not yet reliably matched to available coastal Group 7 South African material.

Onthophagus otjivarongus

Balthasar, 1967

No synonyms
Type locality: 'Süd-West-Afrika, Abachaus, Otjivarongo-District' [Abachaus, Namibia].
Distribution: Namibia.
Notes: Described from female individuals, not matched to available coastal Group 19 Namibian material, but type should be compared to that of *Onthophagus kochi* Frey, 1957 (see *O. kochi* species account).

Onthophagus ovigranosus

Frey, 1971

No synonyms
Type locality: 'Tongaat, Natal' [KwaZulu-Natal, South Africa].
Distribution: South Africa.
Notes: Described from a single female; not yet reliably matched to available Group 22 southern African material from E coast.

Onthophagus pusio

Fahraeus, 1857

No synonyms
Type locality: 'in terra Natalensi' [KwaZulu-Natal, South Africa].
Distribution: South Africa.
Notes: Not placed in a group by d'Orbigny (1913); not matched to available South African material; cited as different to *O. pusio* Péringuey, 1901 (Péringuey 1908).

Onthophagus rubens

d'Orbigny, 1902

= *Onthophagus exiguus* Péringuey, 1892
= *Onthophagus kalaharicus* Kolbe, 1908
Type localities: *O. rubens*, *nom. nov.* for *O. exiguus* (pre-occupied name): type locality not stated; *O. kalaharicus*: 'Kalahari: Lookaneng-Severelela' [Botswana].
Distribution: Namibia, South Africa, Botswana, Zimbabwe; also cited from Lesotho, but presumably an error.
Notes: Not yet reliably matched to available Group 31 southern African material from N Namibia, N Botswana, N South Africa.

Onthophagus rufovirens

d'Orbigny, 1904

No synonyms
Type locality: 'Natal: Durban' [KwaZulu-Natal, South Africa].
Distribution: South Africa.
Notes: Not matched to available Group 2 South African material.

Onthophagus semigraniger

d'Orbigny, 1905

No synonyms
Type locality: 'Sud-Ouest africain: Windhoek' [Namibia].
Distribution: Namibia.
Notes: Not matched to available Group 13 Namibian material.

Onthophagus senescens

Péringuey, 1908

= *Onthophagus seniculus* Péringuey, 1901

Type locality: *O. senescens*, *nom. nov.* for *O. seniculus* (pre-occupied name): 'Ovampoland (Omrramba)' [Ovamboland, Namibia].

Distribution: Namibia.

Notes: Not matched to available Group 16 Namibian material.

Onthophagus setosus

Fahraeus, 1857

= *Onthophagus pedestris* Fahraeus, 1857

= *Onthophagus scabrosus* Fahraeus, 1857

= *Onthophagus cretus* Péringuey, 1901

Type localities: *O. setosus*: 'prope fluvium Limpopo' [near Limpopo River, southern Africa]; *O. pedestris*: 'juxta fluvium Gariep' [near Orange River, South Africa]; *O. scabrosus*: 'juxta fluvium Gariep'; *O. cretus*: 'Natal (Durban, Umkomaas River), Ovampoland (Humbe)' [Durban, KwaZulu-Natal, South Africa; Ovamboland, Namibia].

Distribution: South Africa, Namibia, Angola, Mozambique.

Notes: Not matched to available Group 9 southern African material; validation of species identities required; synonymy of *O. cretus* and citation from Namibia considered errors; see *O. cretus* species account.

Onthophagus simoni

d'Orbigny, 1902

No synonyms

Type locality: 'Hamman's Kraal' [Hammanskraal, Gauteng, South Africa].

Distribution: South Africa, Zimbabwe, Democratic Republic of the Congo (DRC), Tanzania.

Notes: Not matched to available Group 2 southern African material; cited as close to *O. modestus* Harold, 1862.

Onthophagus stenocerus

Harold, 1867

= *Onthophagus gracilicornis* Fahraeus, 1857

Type localities: *O. stenocerus*, *nom nov.* for *O. gracilicornis* (pre-occupied name): 'prope fluvium Limpopo' [near Limpopo River, southern Africa].

Distribution: South Africa, Mozambique.

Notes: Not placed in a group by d'Orbigny (1913); not matched to available material from southern Africa.

Onthophagus sugillatus

Klug, 1855

= *Onthophagus mactatus* Klug, 1855

= *Onthophagus hybridus* Fahraeus, 1857

= *Onthophagus intermedius* Fahraeus, 1857

Type localities: *O. sugillatus*: 'Inhambane' [Mozambique coast]; *O. mactatus*: 'Inhambane'; *O. hybridus*: 'prope fluvium Limpopo' [near Limpopo River, southern Africa]; *O. intermedius*: 'prope fluvium Limpopo'.

Distribution: Mozambique, Namibia, Botswana, South Africa, Lesotho.

Notes: Not reliably matched to available material from southern Africa; Fahraeus synonyms and cited range require validation; at least 10, currently, unnamed species recognised from Group 31 in southern African reference material.

Onthophagus talpa

Fahraeus, 1857

No synonyms

Type locality: 'juxta fluvium Gariep' [near Orange River, South Africa].

Distribution: South Africa, Zimbabwe, Mozambique, Namibia.

Notes: Not placed in a group by d'Orbigny (1913); not matched to available southern African material.

Onthophagus temporalis

d'Orbigny, 1902

No synonyms
Type locality: 'Afrique australe' [southern Africa].
Distribution: South Africa.
Notes: Described from a single female; not matched to available Group 31 southern African material.

Onthophagus ventrosus

d'Orbigny, 1905

No synonyms
Type locality: 'Transvaal' [N South Africa].
Distribution: South Africa.
Notes: Described from a single individual; not matched to available Group 18 South African material.

Onthophagus zumpti

Frey, 1954

No synonyms
Type locality: 'Willowmoore Cape Provinz' [Willowmore, Eastern Cape, South Africa].
Distribution: South Africa.
Notes: Described from three female individuals; not matched to available Group 30 South African material; should be compared with material of *O. cameloides* d'Orbigny, 1900.

SYNTHESIS

A. SYSTEMATICS

Higher classification of the subfamily Scarabaeinae is in disarray due to the degree of polyphyly in the old tribal units comprising the Ateuchini, Canthonini and the possibly older (Monaghan et al. 2007) or possibly more recent tribal unit (Tarasov & Dimitrov 2016) comprising the Coprini. Although some new tribal units are proposed in the most recent global molecular phylogeny of the Scarabaeinae (Tarasov & Dimitrov 2016), revision of the tribal classification system is incomplete. Therefore, the old morphologically based, 12-tribe system (nine tribes in southern Africa) is used for arranging Appendix 3 and the 542 species accounts. However, notes are provided on putative closeness or distance of relationships between genera in each of the three extensively polyphyletic tribes (section B, below).

By contrast, the phylogeny of Tarasov and Dimitrov (2016) is used to arrange Summary Tables 1 and 2 (Appendix 1 and 2). For the three polyphyletic tribes, arrangement is based on the derivation of clades in numbered sequence along the ladderised topology (Figure 5: Clades 1–23). Each clade is further identified according to its placement in the old 12-tribe, morphological classification system. For six primarily monophyletic tribes, arrangement is alphabetical, although each is further identified by clade number.

Topology of the basal dichotomies in the first (Monaghan et al. 2007) and most recent global molecular phylogenies (Tarasov & Dimitrov 2016) differ radically. However, some overall patterns are similar. In the phylogeny of Monaghan et al. (2007), colour coding of basal linkages between clades (Davis et al. 2017) shows no breaks in ancestry for the genera currently assigned to the Ateuchini and Canthonini. The same is clearly true of the phylogeny of Tarasov and Dimitrov (2016) (Figure 5: black basal branches) in which ateuchine and canthonine genera are dispersed throughout the topology in Clades 1–13 and 15–20. They thus form at least part of the membership of most clades except the most terminal. However, bootstrap support is relatively weak for defining relationships at the level of basal nodes in both phylogenies. This in turn weakens support for any current revision of the tribal classification system.

There is, however, often high support for clades at more terminal nodes (see Tarasov & Dimitrov 2016). Each of the 23 clades would represent separate radiations of taxa. Analyses of distribution in southern Africa identify clear differences in pattern bias between some clades. In general, species endemic to the southwest, in the winter rainfall

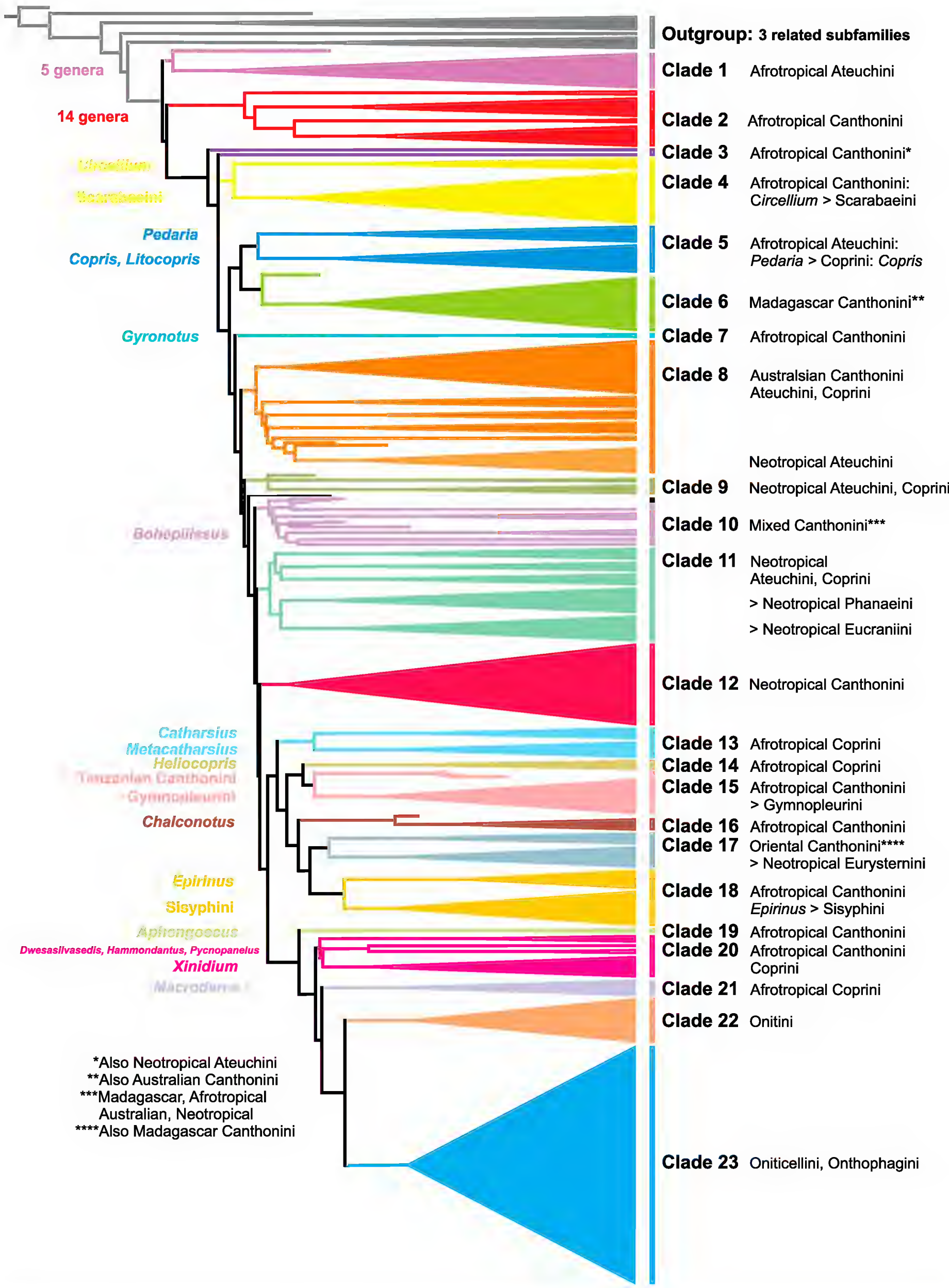


Figure 5. The most recent global molecular phylogeny for the Scarabaeinae after Tarasov and Dimitrov (2016), redrawn, recaptioned and divided into 23 clades used to define groups in the NMDS analyses of Figure 6. Most Canthonini, Ateuchini and Coprini are *incertae sedis* except those designated *sensu novo* by Tarasov and Dimitrov (2016) (includes Ateuchini *pars*). Note that a few *Catharsius* and *Heliocopris* occur in the Oriental region and a few Neotropical genera occur in the Nearctic region.

and desert regions, are most prominent in clades defined for three polyphyletic tribes and the Scarabaeini. The remaining five tribes are mostly centred in the savanna of the summer rainfall region in the northeast (particularly Oniticellini, Gymnopleurini) although a few winter rainfall endemics occur in the Onthophagini, Onitini and Sisyphini. Some also show SW Arid representatives, particularly some Gymnopleurini, Onthophagini and Onitini. A more detailed summary of the patterns follows below.

B. CLADISTIC GROUPS

Distances between spatial distribution patterns have been summarised for all but a few of the species in 542 species accounts using NMDS ordination (Statsoft Inc. 2017) and minimum spanning trees (Excoffier et al. 2006) to connect data points. The analyses were based on the 23 clades defined by the most recent cladistic analysis of relationships within the subfamily Scarabaeinae (Tarasov & Dimitrov 2016, Figure 5). The analysed distribution data for each clade comprised a combined matrix for:

1. Numbers of 1/16th degree squares of latitude and longitude occupied in each of the eight biomes of South Africa.
2. Numbers of 1/16th degree squares occupied in each of 11 main ecoregions for Namibia, Botswana, Zimbabwe and Mozambique within the standard map panel south of 17°S and west of 33°E (see Figure 2 in Introduction).
3. Numbers of 1/16th degree squares occupied in each of the 86, 2° × 2° squares (each = a total of four 1° squares) in the map panel graduated from 17° to 35° S and 12° to 34° E (see Figure 2).

Clades containing large numbers of species were subdivided into taxonomic units (two separate NMDS ordinations for different groups of genera in Scarabaeini; three different NMDS ordinations for the Onthophagini representing different genera or different species groups of *Onthophagus*).

Genera from South Africa, Namibia and Botswana occurred in 16 of the 23 clades defined in the global molecular phylogeny of Tarasov and Dimitrov (2016; Figure 5). Distances between species and geographical distribution centres are summarised by 16 NMDS ordinations (Figure 6). Principal affiliations and geographical patterns are summarised below for each of 13 cladistic groupings or tribes.

Polyphyletic tribes (Clades in numerical order)

Clade 1 (Ateuchini) (Figure 6A): Comprises four out of five genera represented in southern Africa (three Afrotropical, one Afro-Asian) that are classified in the Ateuchini (six genera in total in Africa). Basally derived with (1) *Coptorhina* and *Delopleurus* centred in Highveld Grassland and Savanna with relatives or distributions into the tropics and (2) *Frankenbergerius* and *Sarophorus* with both grassland/savanna and winter rainfall-centred species. All with specialist or putative specialist food associations. Described as part of 'Basal Scarabaeinae' by Tarasov and Dimitrov (2016).

Clade 2 (Canthonini) (Figure 6B): Comprises 14 basally derived Afrotropical genera with specialist habits, all assigned to the Canthonini (in 2017). The very small-bodied, species-rich genus, *Odontoloma*, of unknown habits (possibly kleptocoprid) is equally centred in the summer rainfall and winter plus bimodal rainfall regions with several tropical relatives. The remaining species-poor genera comprise (1) six forest litter taxa along the E escarpment of the Highveld in the summer rainfall region and coastline in the bimodal to winter rainfall regions; and (2) six genera possibly associated primarily with hyrax middens along the arid western seaboard from winter rainfall Namaqualand northwards into Namibia. Described as part of 'Basal Scarabaeinae' by Tarasov and Dimitrov (2016).

Clades 4, 7, 10, 16 (Canthonini) (Figure 6C): Comprises four distantly related Afrotropical genera currently assigned to the Canthonini. Possibly relict or derived with ball-rolling, forest litter or unknown habits. These comprise *Bohepilissus* and *Circellium* (small-bodied, flightless, forest litter genus or large bodied, monotypic and flightless, ball-rolling genus, both in bimodal and winter rainfall regions), *Chalconotus* (savanna and tropical woodland or forest ball-rolling genus), *Gyronotus* (flightless E coast and E escarpment forest or grassland specialist genus of unknown habits).

Clade 5 (Ateuchini, Coprini) (Figure 6D): Comprises both the possibly kleptocoprid, Afrotropical, ateuchine genus, *Pedaria*, and the tunnelling Coprini genera, *Litocopris* and *Copris* (Americas, Afro-Eurasia), but only with 54% bootstrap support. Mostly centred in the summer rainfall region (Savanna, Highveld, NE KwaZulu-Natal coast, N Namibia) with some winter and bimodal

rainfall *Copris* species showing relatives on the Highveld and E coast.

Clades 13, 14 (Coprini) (Figure 6E): Comprises two neighbouring lineages that include three Afro-Eurasian tunnelling genera that are distant from two other clades containing genera assigned to the Coprini. The three genera of Coprini in Clades 13 and 14 comprise large-bodied *Heliocopris*, medium-bodied *Catharsius* and smaller-bodied *Metacatharsius* with the latter more characteristic of the Kalahari. However, all three genera are centred in the summer rainfall region, *Heliocopris* primarily in savanna whereas *Catharsius* appears more diversified eco-geographically.

Clade 18 (Canthonini) (Figure 6F): Comprises the ball-rolling genus, *Epirinus*, which is assigned to the Canthonini ('classic' affiliation), to the Sisyphini (recent transferral by Tarasov and Dimitrov (2016)), or to the tribe Epirinini in a more recent assessment (Daniel et al. 2020). Species are more-or-less equally shared between the winter and bimodal rainfall regions and higher rainfall regions in the summer rainfall region primarily along the E escarpment and E coastal forests.

Clades 19, 20, 21 (Canthonini, Coprini) (Fig 6G): Three neighbouring clades comprising six genera (five Afrotropical, one Afro-Asian) currently assigned to the Canthonini or Coprini that include some genera previously identified as doubtful canthonines (Scholtz & Howden 1987). All genera show restricted distribution patterns and/or specialist habits: *Aphengoecus* (SW Cape-centred, possibly termitophilous (Péringuey 1901)), *Dwesasilvasedis* (monotypic in E coast forest litter), *Hammondantus* (Namib Desert dune specialist), *Macroderes* (flightless, active under cool conditions, primarily in the winter rainfall region), *Pycnopanelus* (SW Arid-centred with conspecifics in Sudan and W Oriental region), the tunnelling *Xinidium* (the only summer rainfall-centred clade member in high altitude grasslands and forest on E escarpment).

Primarily monophyletic tribes (alphabetical order)

Gymnopleurini (Clade 15) (Figure 6H): In the study area, the tribe comprises three Afro-Eurasian or Afro-Asian ball-rolling genera with the tunnelling genus, *Heliocopris*, in a neighbouring clade, but with weak support for the relationship. Species entirely centred in the summer rainfall region, primarily in savanna and SW Arid regions.

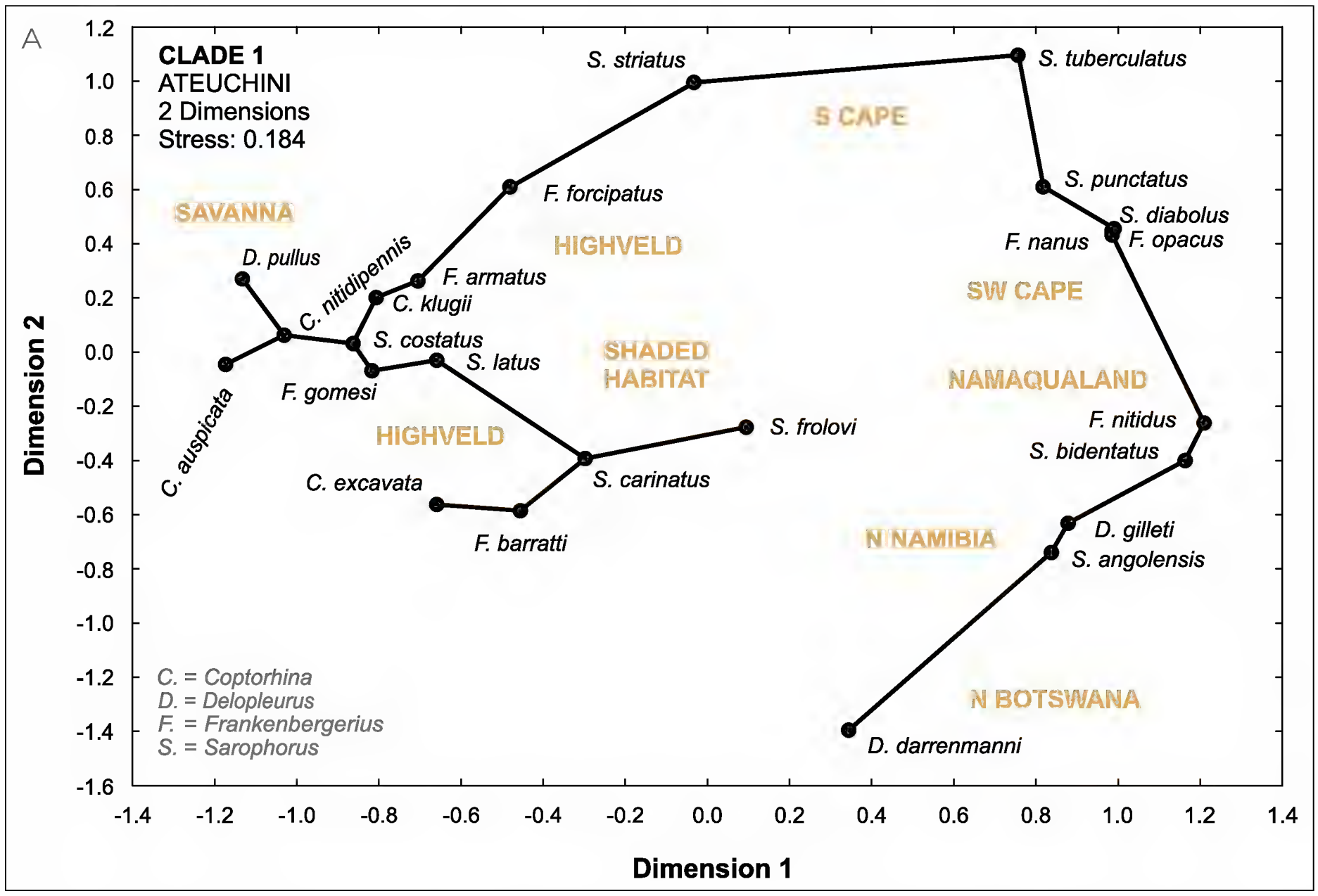
Oniticellini (Clade 23) Figure 6I): In the study area, the tribe comprises 14 tunnelling and endocoprid genera (breed within droppings) (six Afrotropical, six Afro-Asian, two Afro-Eurasian and Americas). Southern African distributions are centred on the summer rainfall region, primarily in savanna and Highveld Grassland with a few in shaded habitats. Strong bias to dung of ruminant or monogastric herbivores in some species.

Onitini (Clade 22) (Figure 6J): In the study area, the tribe comprises 10 tunnelling genera, eight of them species-poor Afrotropical endemics, mostly (seven) associated with monogastric herbivore dung. Two species-rich Afro-Eurasian genera (*Cheironitis*, *Onitis*) include species groups associated with ruminant or monogastric herbivore dung. In southern Africa, species are centred primarily in the summer rainfall region with a bias to the SW Arid region in *Cheironitis* and to savanna or Highveld Grassland in *Onitis* with very few species centred in the winter and bimodal rainfall regions.

Onthophagini (Clade 23) (Figures 6K, 6L, 6M): In the study area, the tribe comprises 15 mainly tunnelling genera (two Afro-Eurasian, five Afro-Asian, seven Afrotropical) including the extremely species-rich, globally distributed genus, *Onthophagus*. Distribution patterns in southern Africa are shown by three separate NMDS ordinations owing to the number of species. The bulk of the distributions are centred in the summer rainfall region, particularly savanna, with some in Highveld Grassland, a few in the SW Arid region, and only six species centred in the winter and bimodal rainfall regions (out of a total of 123).

Scarabaeini (Clade 4) (Figures 6N, 6O): In the study area, the tribe comprises seven primarily ball-rolling genera with Afrotropical (4), Afro-Eurasian (2) or Afro-Asian (1) distributions. Distribution patterns in southern Africa are shown by two separate NMDS ordinations owing to the number of species. There is a distinct SW distributional bias in most genera although most have relatives in the tropics. However, all genera show a few or many winter rainfall representatives. Distribution is restricted to the W coast in flightless *Pachysoma*, from the winter rainfall region northwards into Namibia. SW distributional bias is strong in small-bodied *Scarabaeolus* (winter rainfall region, SW Arid, Kalahari, a few on the E coast). SW and NE bias is roughly even in mostly larger-bodied *Scarabaeus*, *Sceliages* and *Escarabaeus* whereas NE bias dominates in *Pachylomera* and in *Kheper*, which shows various tropical relatives.

Sisyphini (Clade 18) (Figure 6P): In the study area, the tribe comprises two ball-rolling genera (one Afro-Asian, one Afro-Eurasian and Americas) with southern African distributions mostly centred in the mid-summer rainfall region, primarily savanna and Highveld Grassland. Recent changes reduce the two genera to a single genus comprising three subgenera all, of which, occur within the study area (Daniel et al. 2020).



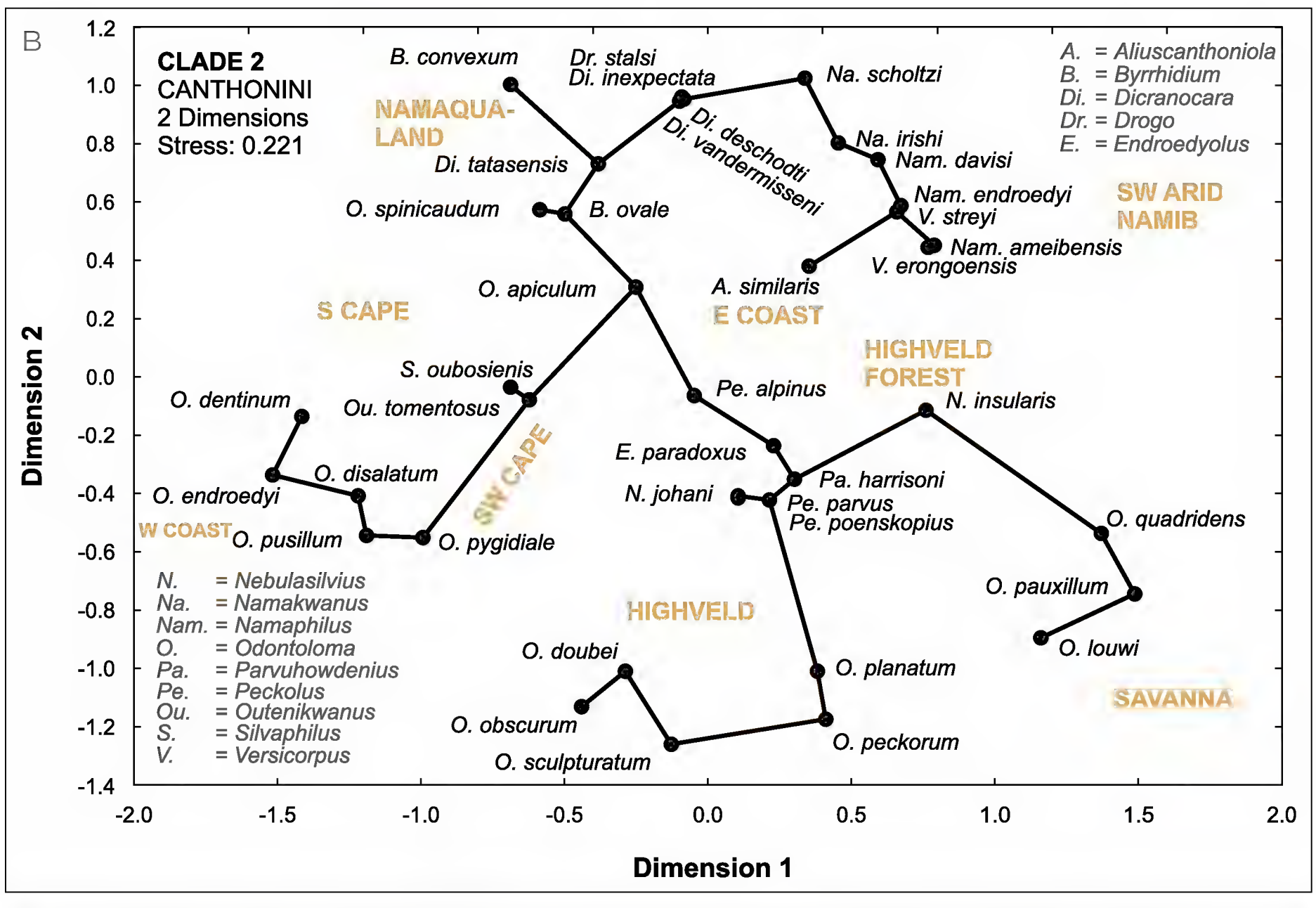
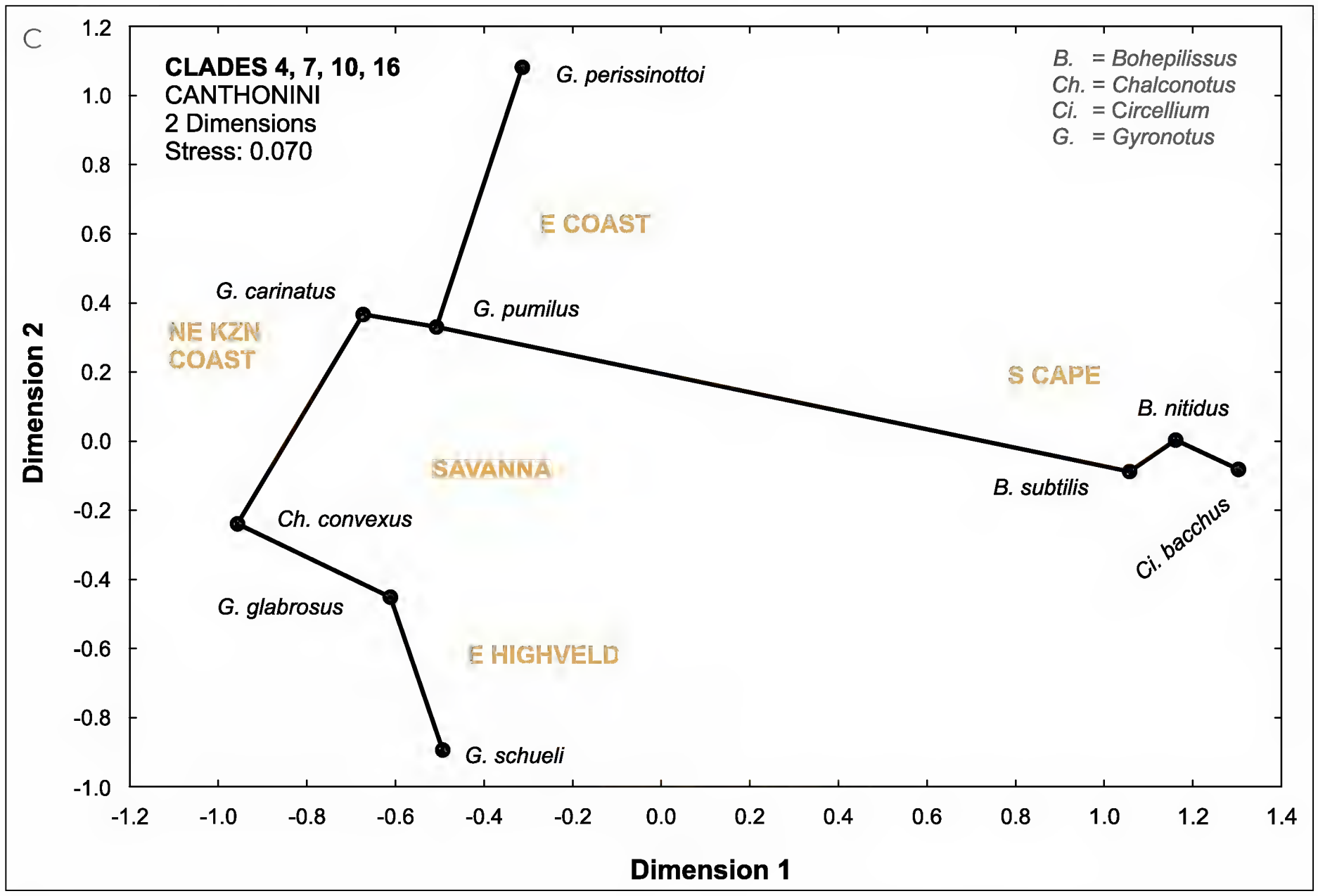


Figure 6. NMDS and Minimum Spanning Tree representation of statistical distances between species distribution patterns within the standard distribution map panel: A, Clade 1 (Ateuchini); B, Clade 2 (Canthonini).



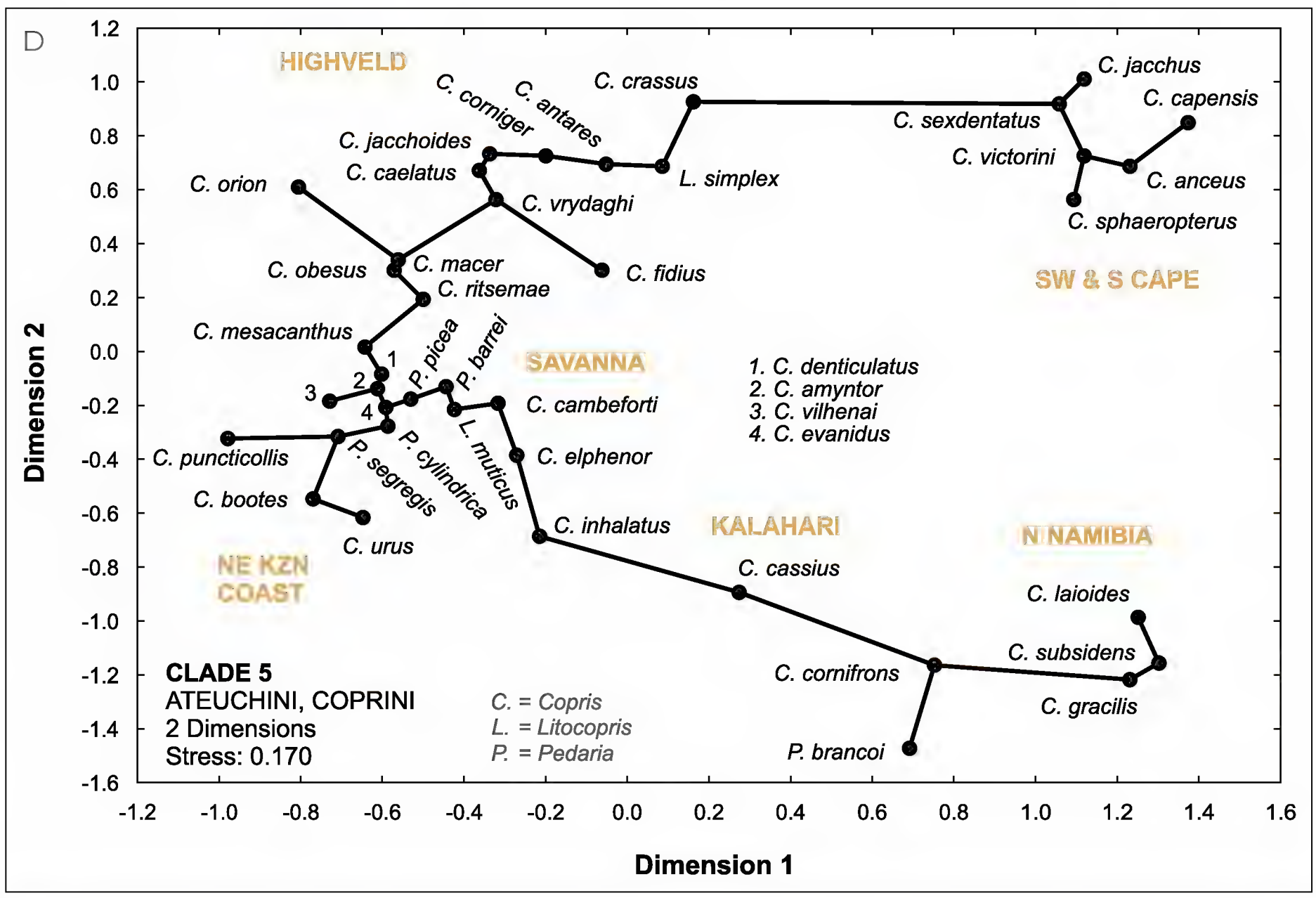


Figure 6 (continued). NMDS and Minimum Spanning Tree representation of statistical distances between species distribution patterns within the standard distribution map panel: C, Clades 4, 7, 10 and 16 (Canthonini); D, Clade 5 (Ateuchini, Coprini).

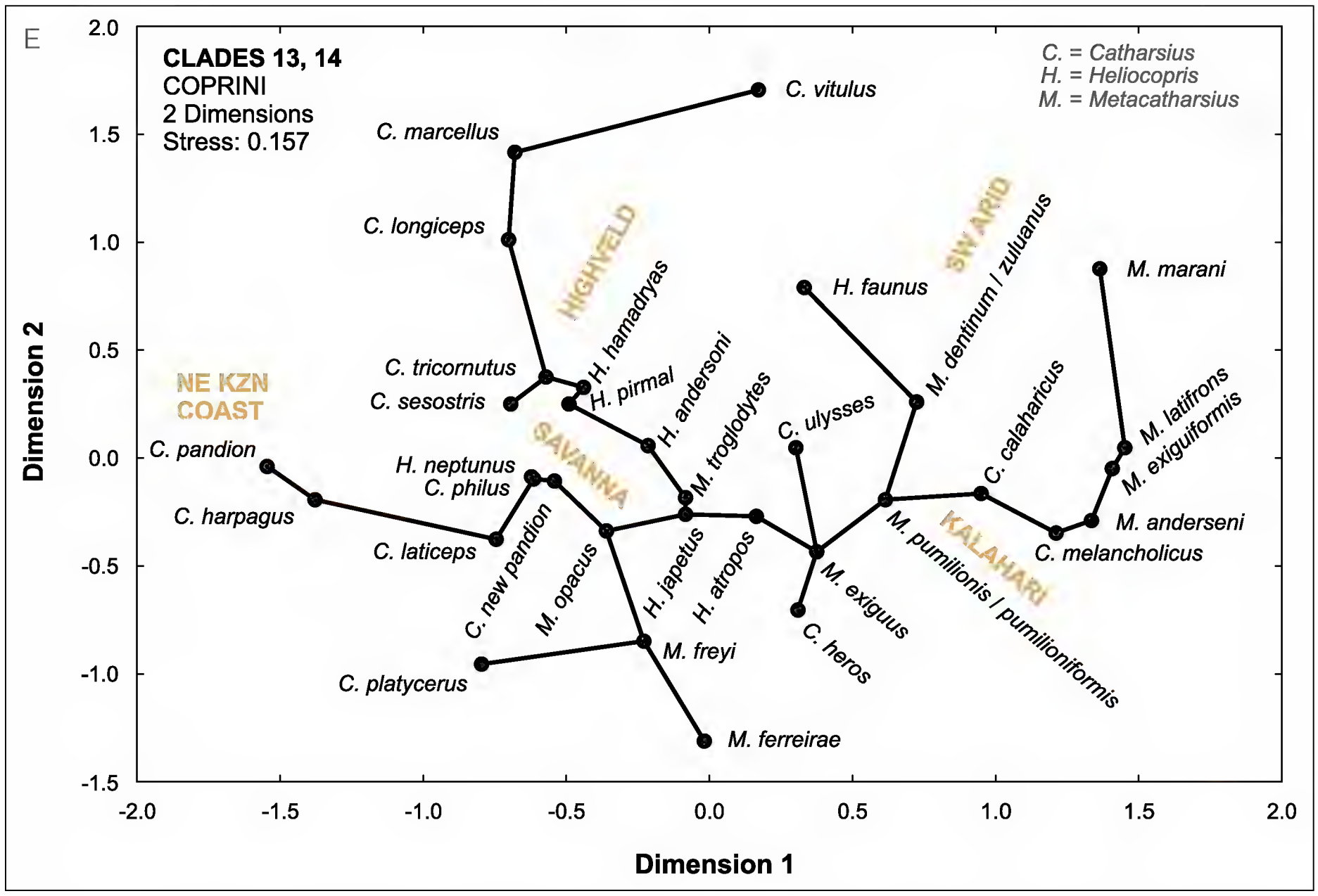
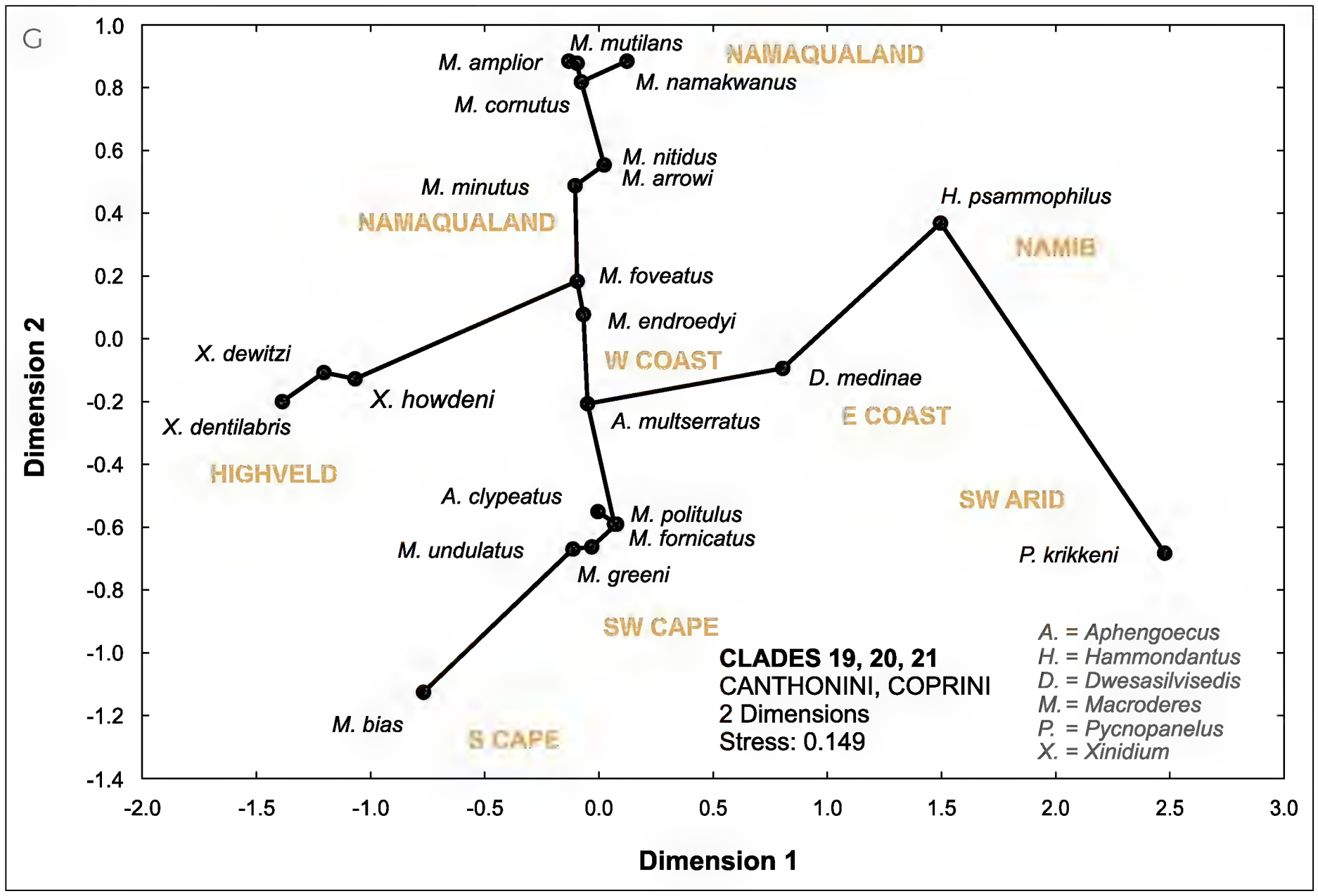


Figure 6 (continued). NMDS and Minimum Spanning Tree representation of statistical distances between species distribution patterns within the standard distribution map panel: E, Clades 13, 14 (Coprini); F, Clade 18 (Canthonini).



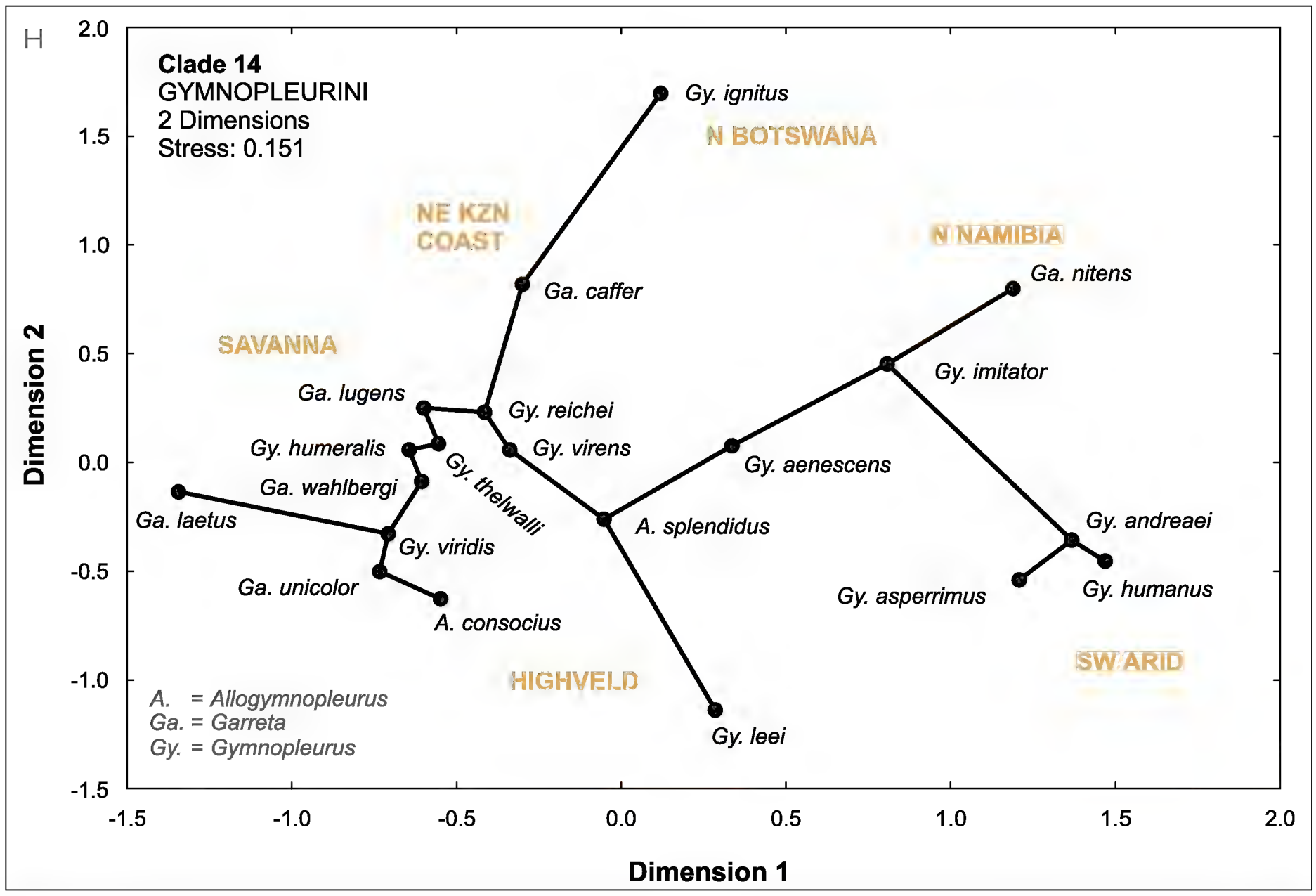
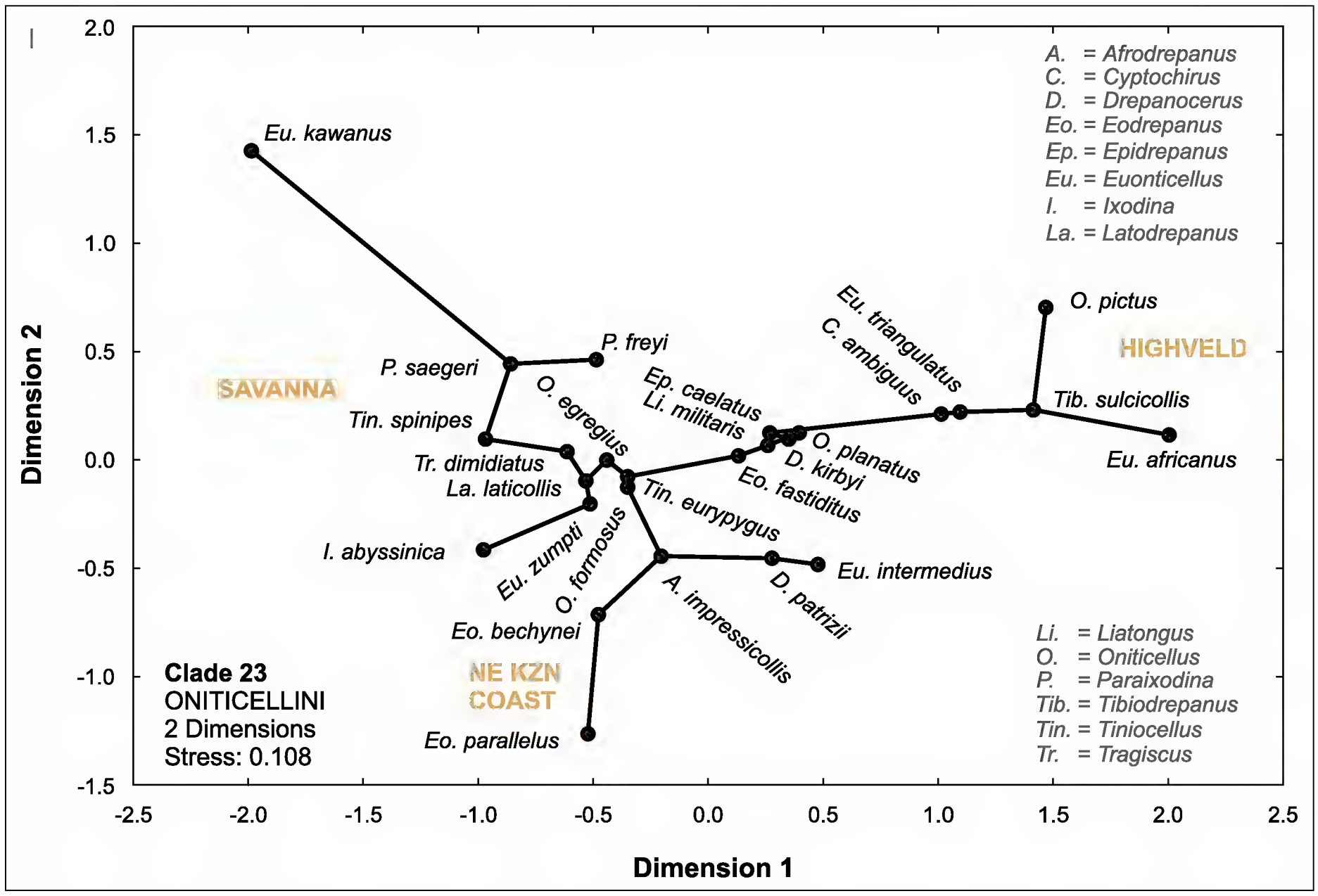


Figure 6 (continued). NMDS and Minimum Spanning Tree representation of statistical distances between species distribution patterns within the standard distribution map panel: G, Clades 19, 20, 21 (Canthonini, Coprini); H, Gymnopleurini (Clade 14).



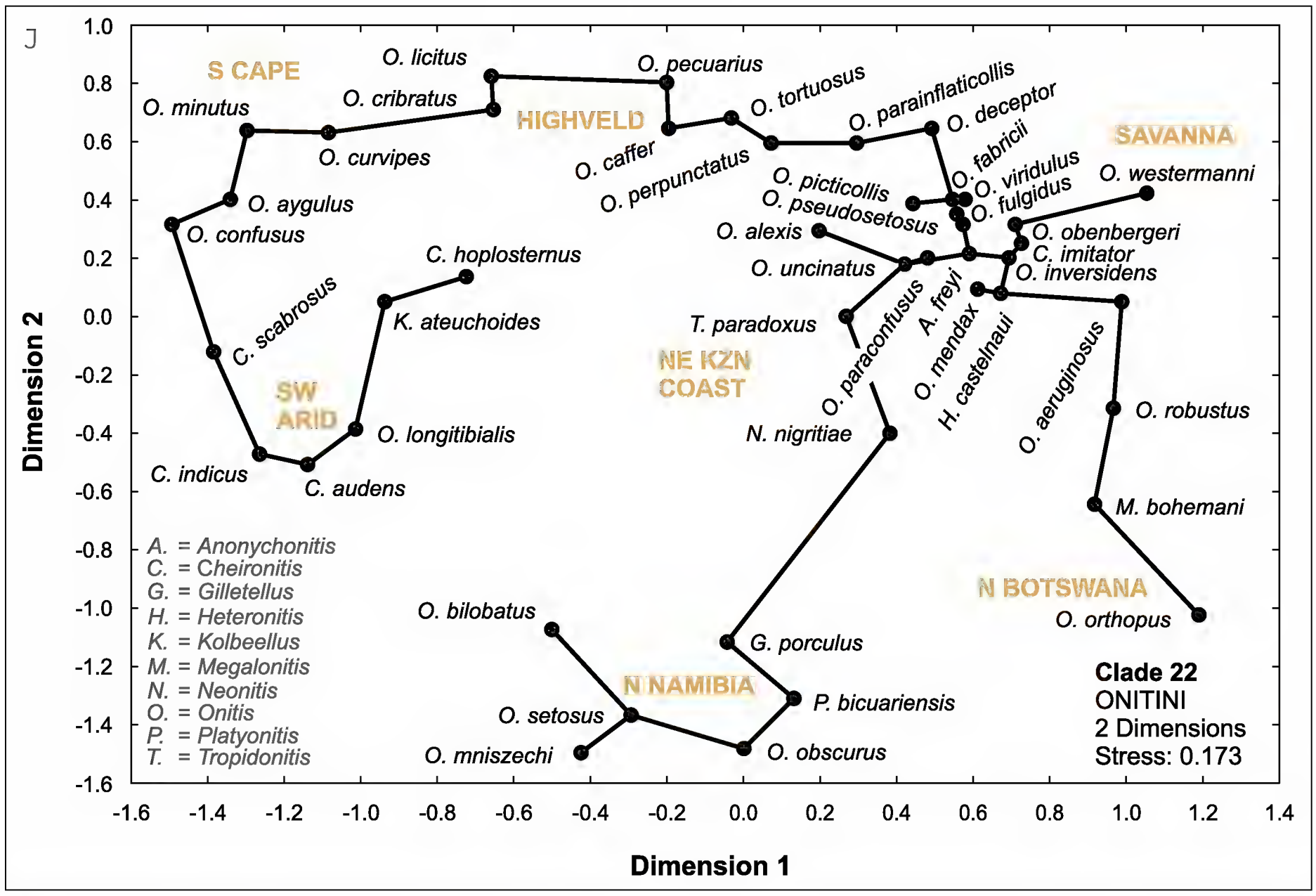


Figure 6 (continued). NMDS and Minimum Spanning Tree representation of statistical distances between species distribution patterns within the standard distribution map panel: I, Oniticellini (Clade 23); J, Onitini (Clade 22).

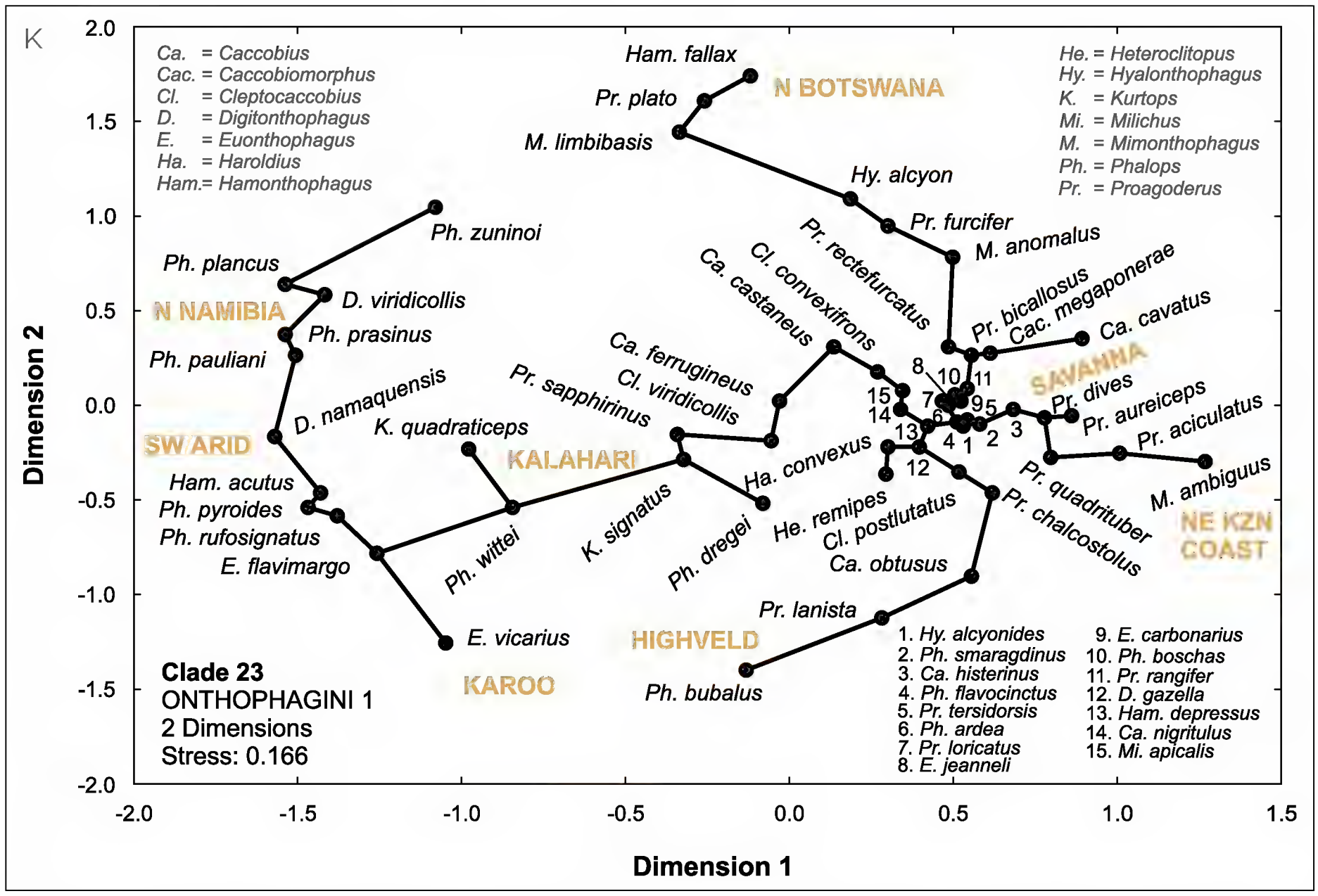
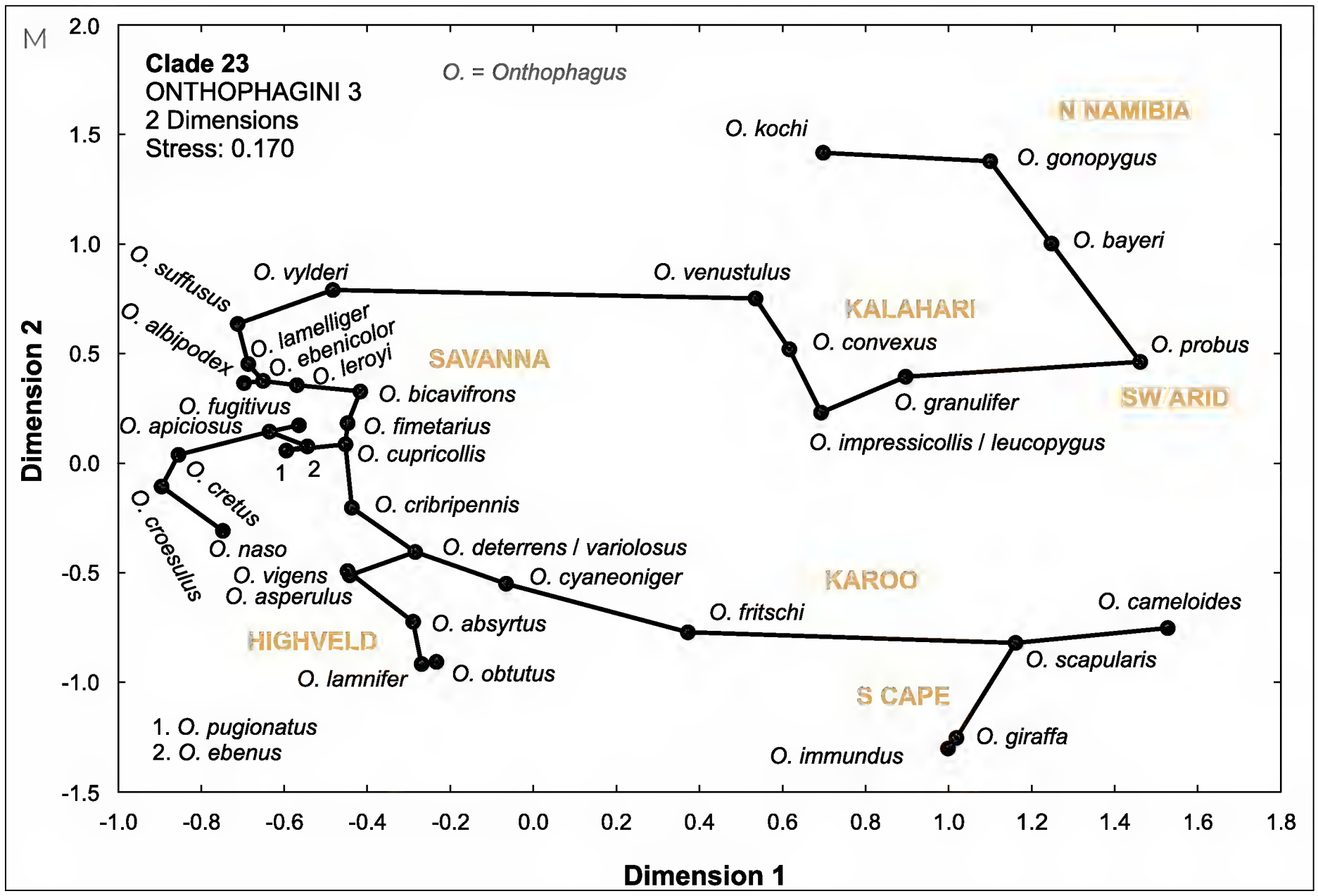


Figure 6 (continued). NMDS and Minimum Spanning Tree representation of statistical distances between species distribution patterns within the standard distribution map panel: K, Onthophagini 1 (Clade 23); L, Onthophagini 2 (Clade 23, species groups 2–16).



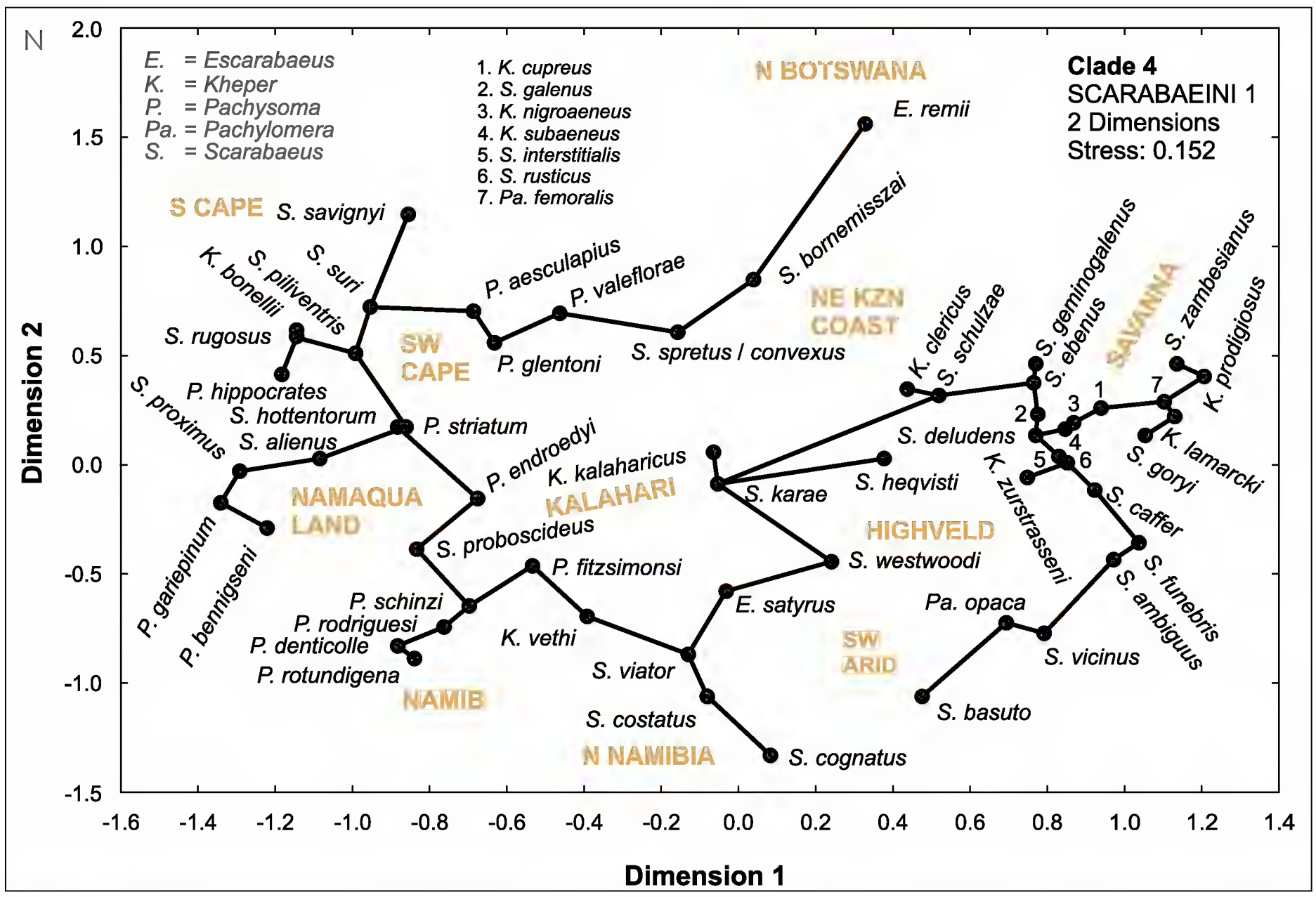
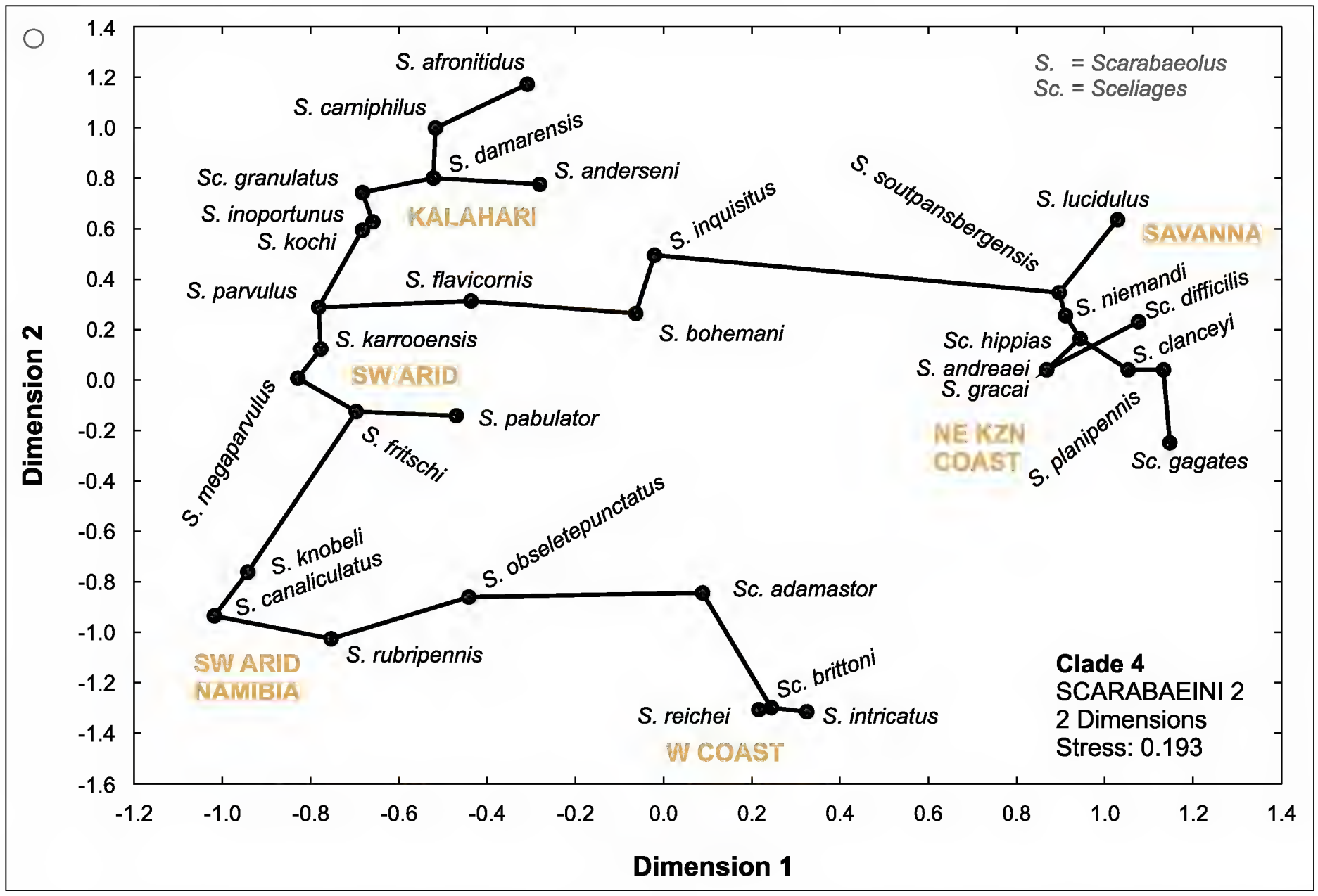


Figure 6 (continued). NMDS and Minimum Spanning Tree representation of statistical distances between species distribution patterns within the standard distribution map panel: M, Onthophagini 3 (Clade 23, species groups 17–31); N, Scarabaeini 1 (Clade 4).



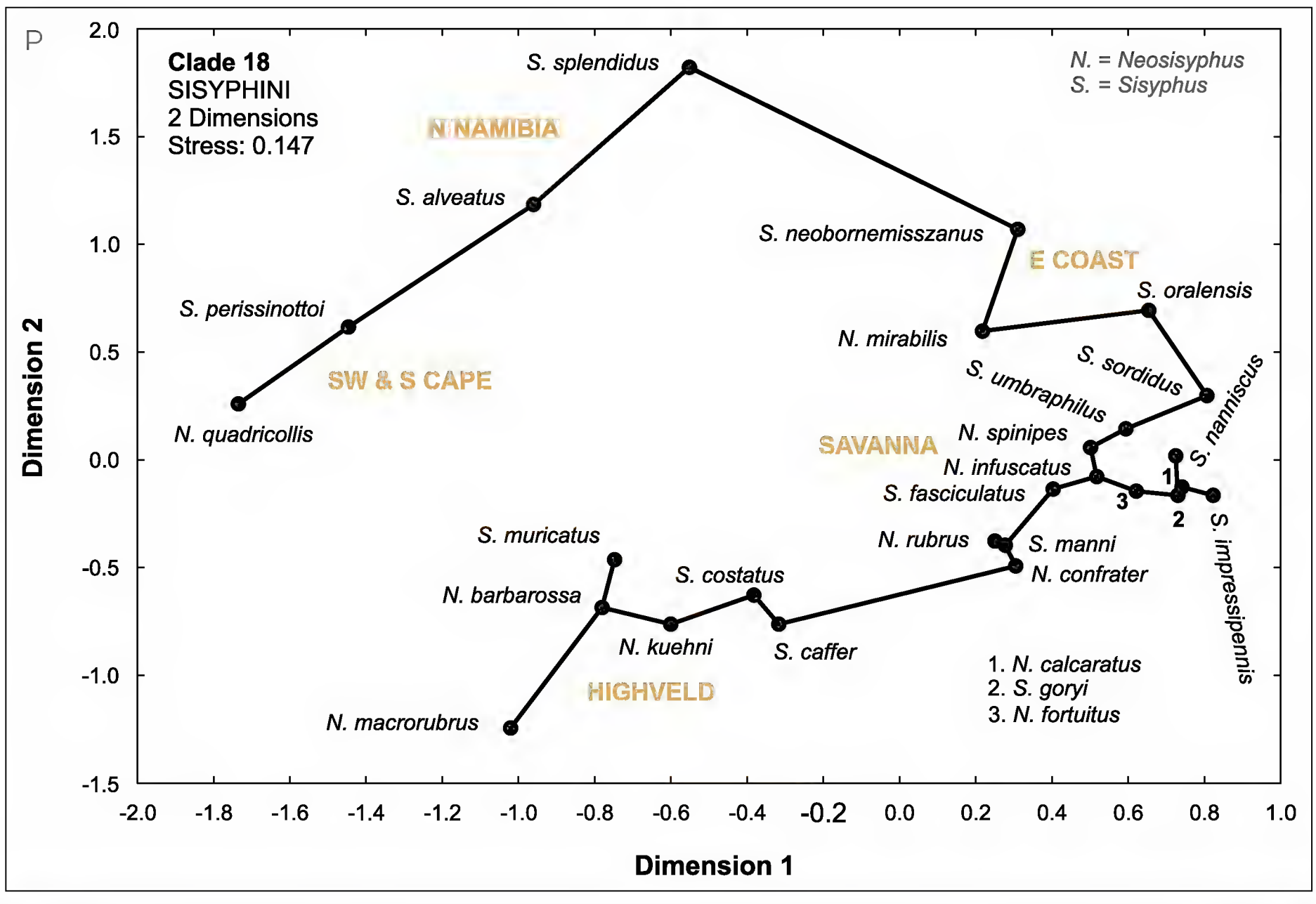


Figure 6 (continued). NMDS and Minimum Spanning Tree representation of statistical distances between species distribution patterns within the standard distribution map panel: O, Scarabaeini 2 (Clade 4); P, Sisyphini (Clade 18).

C. MAJOR SPATIAL PATTERNS

Geographical ranges varied from very small to very large. A number of distinct regional distribution patterns were recognised for species showing intermediate range sizes and these are described below. Further localisation and smaller range size within these patterns were driven by climate, soil and/or vegetation type specialisation. At the opposite extreme, larger range size was shown by species with more generalist, widespread associations. These occurred across different combinations of the intermediate-sized regional patterns.

Examples of some more common widespread patterns:

1, 2. **(SW Cape, S Cape):** *Epirinus comosus*, *Odontoloma dentinum*, *Sarophorus tuberculatus*, *Onthophagus giraffa*.

2, 3. **(Highveld, S Cape):** *Sisyphus costatus*, *Onitis caffer*, *Onthophagus binodis*, *Oniticellus pictus*.

2, 3. **(Highveld, E Escarpment, S Cape):** *Epirinus relictus*, *Neosisyphus barbarossa*, *Sisyphus muricatus*.

3, 4. **(Highveld, E Coast):** *Onitis pecuarius*, *Cyptochirus ambiguus*, *Euoniticellus triangulatus*.

3, 5. **(Highveld, Upper Karoo):** *Scarabaeus basuto*, *Catharsius vitulus*, *Phalops bubalus*, *Onthophagus cyaneoniger*.

4, 7. **(E coast, E savanna):** *Heliocopris hamadryas*, *Onthophagus cribripennis*.

4, 7. **(NE KZN coast, E savanna):** *Pedaria segregis*, *Sisyphus sordidus*, *Phalops flavocinctus*.

Examples of some rarer, but distinctive widespread patterns:

3, 4, 7. **(Highveld, E coast, savanna):** *Onitis alexis*, *Onthophagus aeruginosus*, *Liatongus militaris*.

1, 2, 5. **(SW and S Cape, Upper Karoo):** *Epirinus aeneus*, *Onthophagus cameloides*.

1, 6. **(SW Cape W Coast / Namaqualand, Kalahari):** *Scarabaeolus flavicornis*, *Metacatharsius latifrons*.

3, 4. **(NE KZN coast / Highveld E escarpment):** *Sisyphus fasciculatus*, *Afrodrepanus impressicollis*.

3, 7. **(Highveld / N Namibia):** *Scarabaeus ambiguus*, *Catharsius ulyssses*, *Neosisyphus macrorubrus*, *Proagoderus lanista*.

5, 7. **(Savanna (E & W), Upper Karoo):** *Scarabaeolus bohemani*, *Heliocopris faunus*, *Onthophagus bovinus*.

Endemic patterns: South Africa

1. **SW Cape:** Centred on the winter rainfall region (Figure 7D); localisation within pattern due to soil (sand/finer-grained), vegetation (forest, shrubland, scrub, disturbed patches), climate (coastal lowlands or mountain). Distinct sub-pattern on W Coast caused by increasing aridity from S to N (Namaqualand) (Figure 7B) and by changing edaphic character from W to E (sand to finer-grained soils and cooler climate above W escarpment) (SW CAPE, W COAST, NAMAQUALAND).

   Examples of the patterns are:
   - **SW Cape:** *Scarabaeus suri*, *Scarabaeus intricatus*, *Odontoloma pygidiale*, *Sarophorus diabolus*.
   - **W Coast:** *Scarabaeolus reichei*, *Scarabaeus rugosus*, *Pachysoma hippocrates*, *Epirinus scrobiculatus*.
   - **Namaqualand:** *Byrrhidium ovale*, *Pachysoma striatum*, *Scarabaeus hottentorum*, *Macroderes namakwanus*, *Macroderes mutilans*.

2. **S Cape:** Centred on the bimodal spring/autumn rainfall region (Figure 7D); localisation within pattern due to soil (sand/finer-grained), vegetation (forest, shrubland, scrub), climate (winter to bimodal rain from W to E) (S CAPE).

   Examples of the pattern are:
   - **S Cape:** *Circellium bacchus*, *Scarabaeus savignyi*, *Copris jacchus*, *Sarophorus striatus*, *Sisyphus perissinottoi*.
   - **S Cape Forest:** *Bohepilissus subtilis*, *Epirinus silvestris*.

3. **Highveld:** Centred on the Grassland Biome (Figure 3); localisation within pattern due to increasing rainfall and higher altitude from W to E. Leads to distinct drier NW, W or wetter SE or E escarpment sub-patterns; some species are endemic to forest patches at different points along escarpment in the E and SE (HIGHVELD, HIGHVELD FOREST).

   Examples of the patterns are:
   - **Highveld:** *Coptorhina excavata*, *Copris antares*, *Copris corniger*, *Onthophagus obtutus*.
   - **Highveld (NW):** *Epirinus gratus*.
   - **Highveld (SE):** *Epirinus obtusus*.
   - **Highveld (E):** *Epirinus asper*, *Epirinus validus*, *Copris caelatus*, *Catharsius marcellus*.
   - **Highveld Forest (edge of E or SE Escarpment):** *Epirinus punctatus*, *Frankenbergerius armatus tuberculatus*, *Xinidium dewitzi*, *Peckolus alpinus*, *Endroedyolus paradoxus*.

Shared pattern: South Africa, Mozambique

4. **E Coast:** Centred on the moist, E coastal belt (Figure 3); localisation within pattern due to soil (sand/finer-grained), vegetation (forest, woodland grassland), occurrence of reserves with indigenous monogastric herbivores; distinct sub-pattern in warmer NE (Figs 6C, 6D) that continues northwards into the tropics (E COAST, NE KZN COAST, FOREST).

   Examples of the patterns are:
   - **E Coast:** *Gyronotus pumilus*, *Copris orion caffer*, *Mimonthophagus ambiguus*, *Onthophagus cretus*.
   - **NE KZN Coast:** *Kheper clericus*, *Anonychonitis freyi*, *Copris inhalatus sanctaluciae*, *Tropidonitis paradoxus*.
   - **NE KZN Coast Forest:** *Gyronotus carinatus*, *Scarabaeus bornemisszai*, *Sisyphus neobornemisszanus*, *Garreta caffer*.

Shared patterns: South Africa, Namibia, Botswana

5. **SW Arid:** Centred on the arid late summer rainfall region (Figure 7D), primarily in South Africa and Namibia; localisation within pattern due to soil (sand/finer-grained), particularly sand on outlier Kalahari dunes and in saline pans in South Africa. Also, a N to S climatic gradient from cooler to warmer and drier to moister conditions (Figures

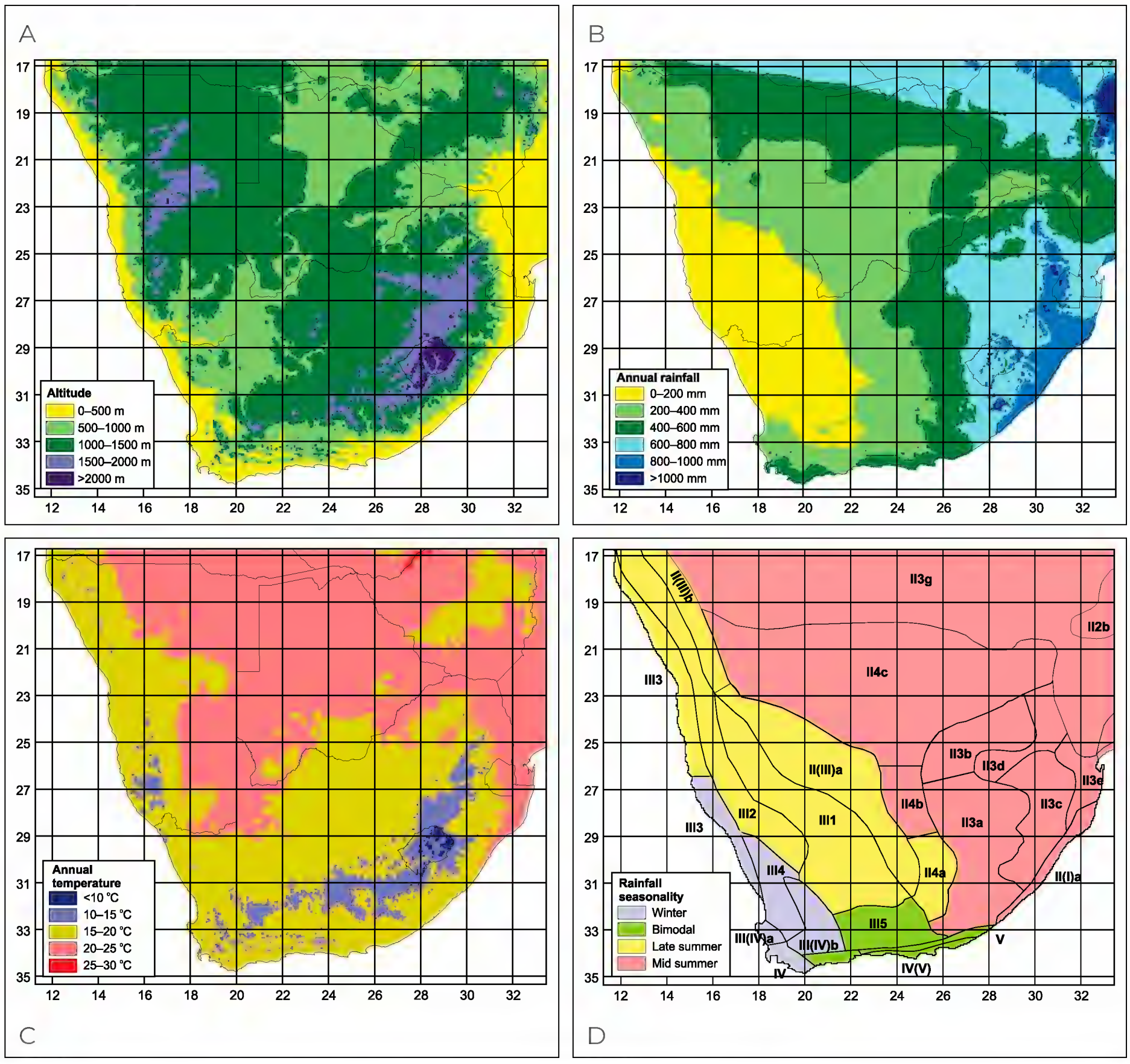


Figure 7. A, Altitude; B, Annual rainfall; C, Annual temperature (max. + min. / 2); D, Rainfall seasonality and climatic regions after Walter and Lieth (1964) across the standard distribution map panel (see Figure 2).

7B, 7C) resulting in distinct sub-patterns at higher altitude on the Upper Karoo in South Africa and sub-patterns in the Namib and Kaokoveld Deserts in Namibia with increasing coastal coolness from E to W (SW ARID, KAROO, NAMIB).

Examples of the patterns are:

- **SW Arid:** *Pycnopanelus krikkeni*, *Gymnopleurus humanus*, *Gymnopleurus asperrimus*, *Metacatharsius marani*, *Onthophagus semiflavus*.
- **Upper Karoo:** *Epirinus striatus*, *Scarabaeus viator*, *Euonthophagus vicarius*, *Onthophagus peringueyi*.
- **Namib Desert:** *Pachysoma denticolle*, *Pachysoma rodriguesi*, *Scarabaeolus rubripennis*, *Hammondantus psammophilus*.
- **N Namib-Kaokoveld:** *Kheper vethi*, *Scarabaeus cognatus*, *Scarabaeolus namibensis*, *Phalops plancus*.

6. **Kalahari:** Centred on hot, deep sands of the Kalahari in central southern Africa with localisation due to increasing aridity to the SW (Figures 7B, 7C) (KALAHARI).

   Examples of the patterns are:
   - **SW Kalahari:** *Scarabaeolus inoportunus*, *Metacatharsius anderseni*, *Copris cornifrons*, *Euonthophagus flavimargo*.
   - **Kalahari:** *Catharsius calaharicus*, *Kurtops quadraticeps*, *Proagoderus sapphirinus*, *Onthophagus granulifer*.

7. **Savanna:** Centred on moist to dry savanna (Figure 3) in northern regions of southern Africa (Namibia, Botswana, South Africa); many species are biased to the E, some to the W, whereas some occur in both the E and W; many savanna distributions continue into the tropics. Localisation within the pattern due to soil (sand/finer-grained), vegetation (forest, woodland, shrubland, grassland), occurrence of reserves with indigenous monogastric herbivores and/or climate. Local patterns along the E–W trending Waterberg, Soutpansberg and N edge of Highveld in South Africa; also N Namibian Plateau and N Botswana Basin (SAVANNA, N NAMIBIA, N BOTSWANA).

   Examples of the patterns are:
   - **Savanna (E & W):** *Copris elphenor*, *Onitis uncinatus*, *Onthophagus suffusus*, *Oniticellus egregius*.
   - **E Savanna:** *Garreta wahlbergi*, *Catharsius philus*, *Copris amyntor*, *Onitis viridulus*, *Onthophagus lamelliger*.
   - **Savanna game reserves:** *Onitis mendax*, *Proagoderus rangifer*, *Proagoderus rectefurcatus*, *Euonthophagus jeanneli*.
   - **Soutpansberg:** *Scarabaeus schulzeae*.
   - **Waterberg:** *Onthophagus cupricollis*.
   - **N Botswana:** *Escarabaeus remii*, *Frankenbergerius darrenmanni*.
   - **N Namibia (W Savanna):** *Copris laioides*, *Copris subsidens*, *Phalops prasinus*, *Phalops pauliani*.

D. CLIMATE, SAMPLING AND GEOGRAPHICAL BIAS

Patterns of species numbers and distribution show clear differences across the standard map panel (Figures 8, 9, 10). These differences are due partly to uneven intensity of collecting (Figure 10A) and partly to geographical variation in altitude, annual rainfall, annual temperature and rainfall seasonality (Figures 7A–7D).

Depictions of collecting intensity are based on the reference collections of the National Collection of Insects, Ditsong Museum, University of Pretoria and selected published or unpublished survey data. Collecting intensity has been high along the coastline and in the NE of South Africa as well in parts of the Northern Cape. However, the absence of records across much of the Karoo and SW Highveld have certainly resulted in lower observed numbers of species than would be expected in some areas. In Namibia and Botswana, intensity of collection has been lower than in South Africa (Figure 10A). Collecting has been concentrated along the SW desert coastline and N plateau in Namibia and along major roads in Botswana. Large areas lack collections particularly most of the NE and E of Namibia and most of the Kalahari system in Botswana. However, a few areas of higher sampling and/or collecting intensity stand out as regards numbers of species (Figure 10D), i.e. NE Botswana, Northern Cape and NE South Africa.

Comparisons between the nine tribes suggests three main patterns of species number distribution across South Africa, Botswana and Namibia (Figure 9). Seven tribes (Figures 8A, 8C–8G, 8I) show highest numbers of species mostly in the NE savanna of South Africa where there is high collecting intensity (Figure 10A), high topographical and temperature diversity and relatively high summer rainfall (Figures 7A, 7B, 7C). Of these tribes, the Ateuchini, Sisyphini, and to a lesser extent, the Oniticellini show a particularly strong bias to the moister regions in the E

(Figures 7B, 8A, 8E, 8I), which may reflect their ecological associations. The Onitini, Coprini, and, to a lesser extent, the Onthophagini, are also fairly well represented in other savanna regions in the Northern Cape, N Botswana and N Namibia (Figures 8C, 8F, 8G). The Gymnopleurini are also fairly well represented by specialist species in the arid SW, but are absent from the SW winter rainfall region (Figures 7B, 7D, 8D), unlike the other eight tribes. The Scarabaeini, and particularly the Canthonini, show quite different patterns to the other seven tribes. In savanna regions, the Scarabaeini are well represented only in South Africa, but they are particularly diverse in arid climates along the W seaboard of southern Africa although poorly represented on the SE seaboard (Figure 8H). The Canthonini are centred primarily in cooler regions from the SW Cape along the S coast and up the E escarpment that borders the Highveld (Figure 8B). Fewer species occur locally on the South African highlands and the arid escarpment regions along the W seaboard. It should be noted that only the Scarabaeini, Coprini and Onthophagini, show appreciable numbers of species on the deep sands of the S Kalahari Basin (Figures 8C, 8G, 8H).

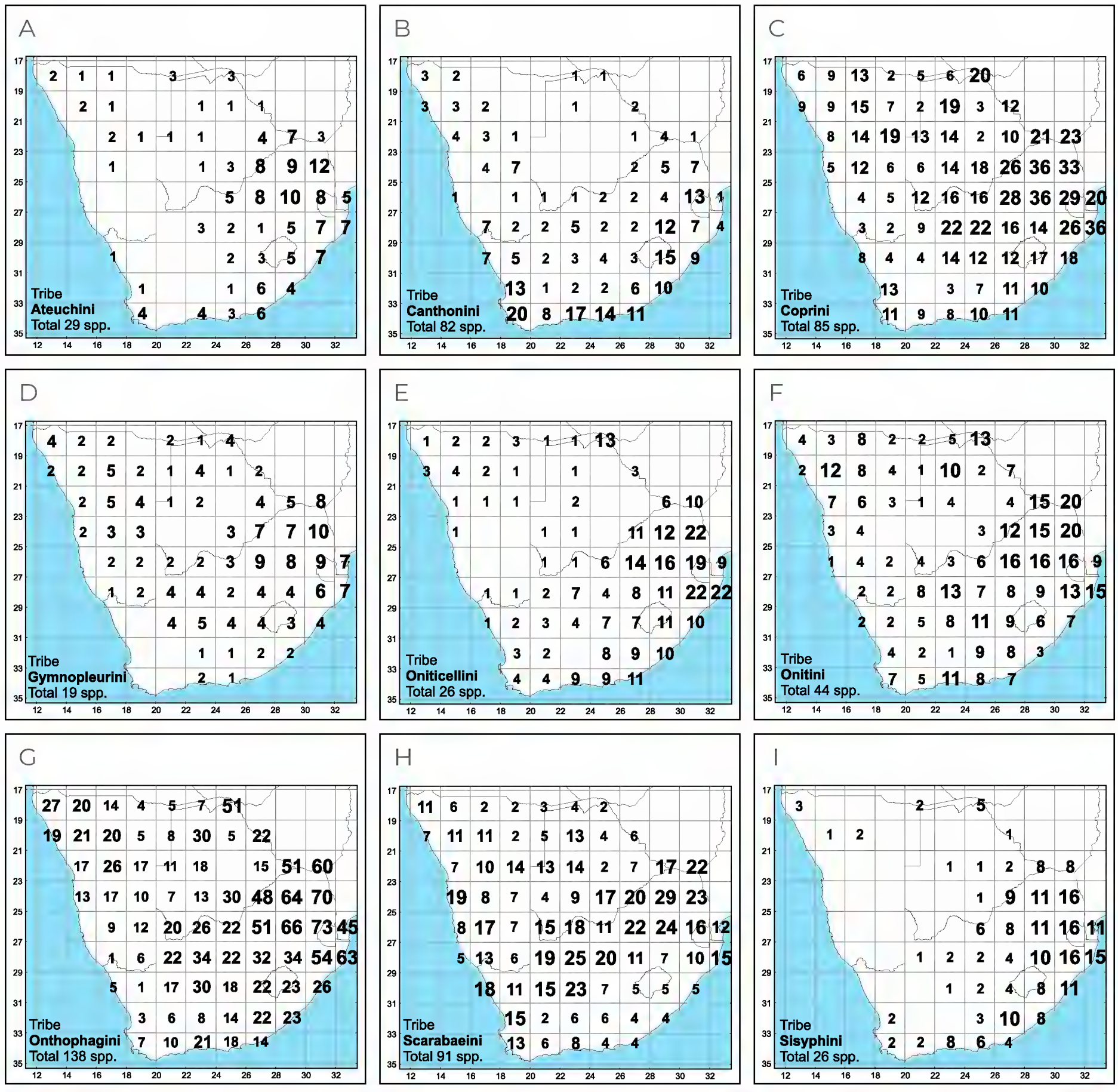


Figure 8. Numbers of scarabaeine dung beetles species per 4° square (2×2 1° squares) within the standard distribution map panel (see Figure 1): A, Tribe Ateuchini; B, Tribe Canthonini; C, Tribe Coprini; D, Tribe Gymnopleurini; E, Tribe Oniticellini; F, Tribe Onitini; G, Tribe Onthophagini; H, Tribe Scarabaeini; I, Tribe Sisyphini (large text = 50–100% of square with maximum number of species (maxima: A=12, B=20, C=36, D=10, E=22, F=20, G=73, H=29, I=16), medium text = 25–50%, small text = 0–25%).

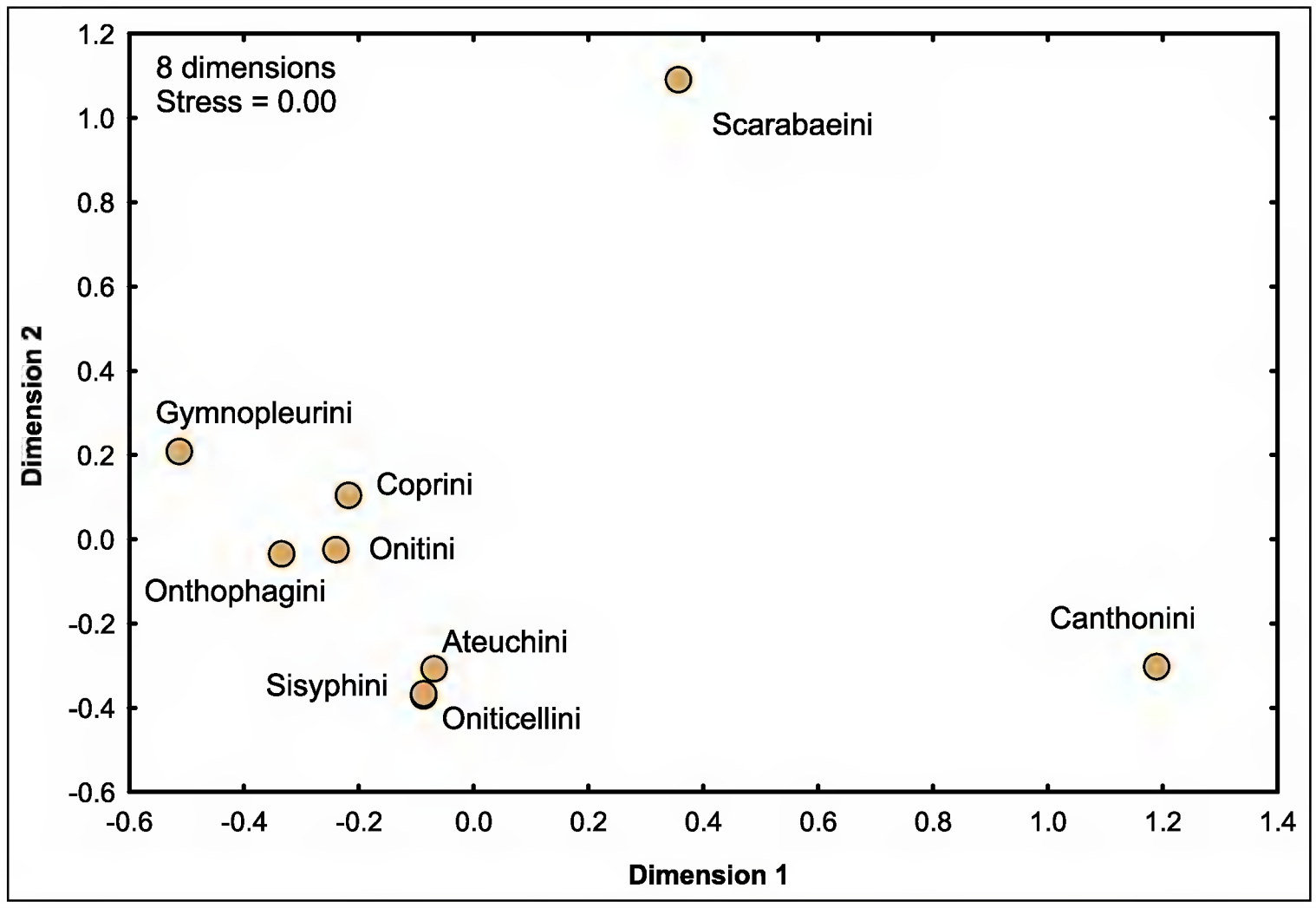


Figure 9. MDS ordination plot showing statistical distances between the patterns of species number distribution across South Africa, Botswana and Namibia (Figures 8A–8I) in nine dung beetle tribes.

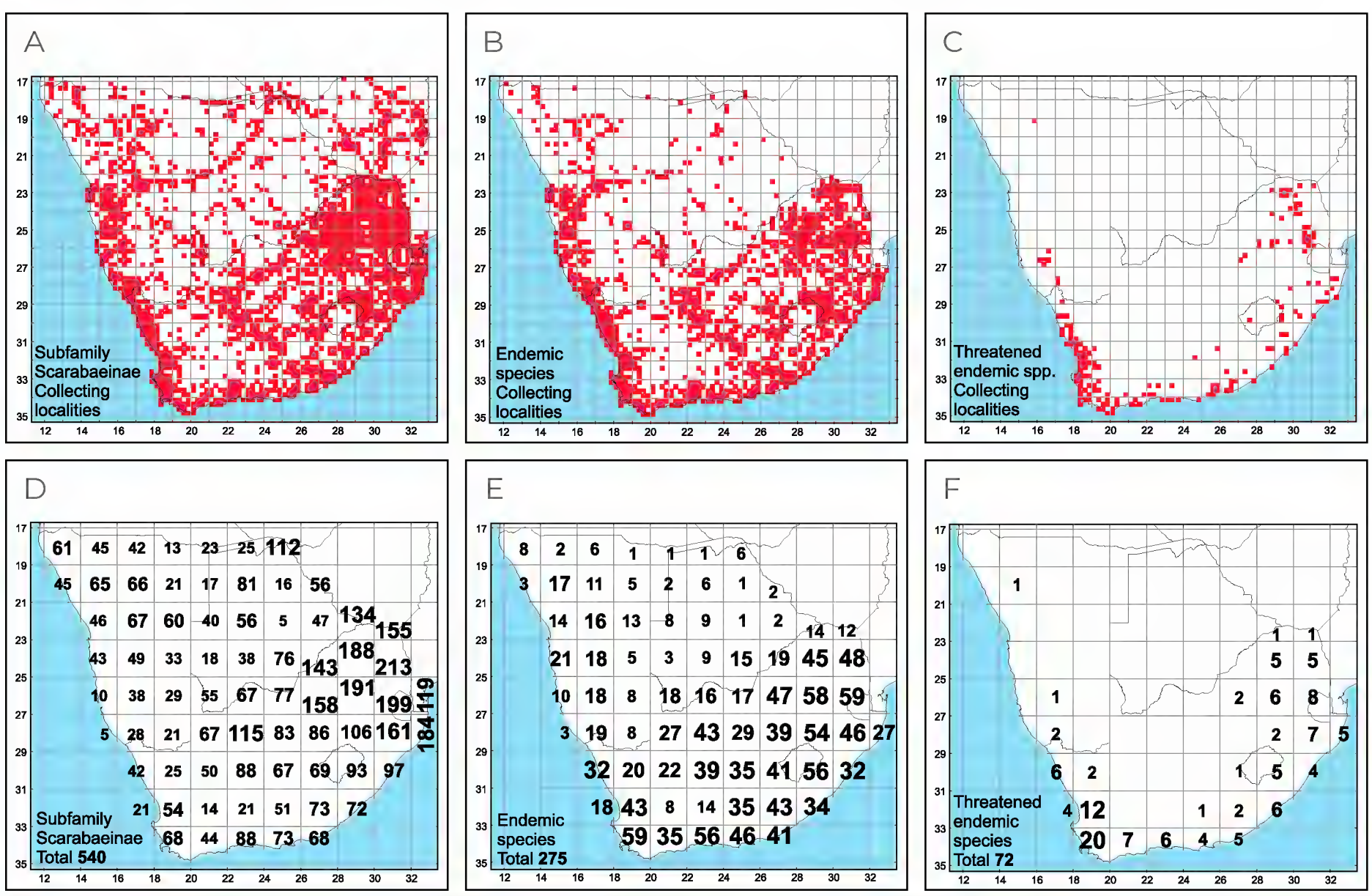


Figure 10. Collection localities of scarabaeine dung beetles represented by 1/16th of a degree squares: A, Squares in which dung beetles were collected; B, Squares in which dung beetles endemic to South Africa, Botswana and/or Namibia were collected; C, Squares in which threatened endemic dung beetle species were collected; D, 540 species of the Subfamily Scarabaeinae; E, Species endemic to South Africa, Botswana and/or Namibia; F, Threatened endemic species (large text = 50–100% of square with maximum number of species (maxima: D=213, E=59, F=20), medium text = 25–50%, small text = 0–25%).

E. CLIMATE, ENDEMISM AND CONSERVATION

Based on available spot distribution data, just over half of 540 species (Figures 10A, 10D) were considered to be endemic to South Africa, Botswana and/or Namibia (Figures 10B, 10E). Putative endemic species were recorded across the entire area of the three countries. Numbers of endemics in the SW of South Africa were frequently similar to numbers in the NE. However, for example, the 59 or 43 species recorded in the 4° squares near Cape Town (Figure 6SD, 6SE) represented 86.8% and 79.6% endemism compared to the 59 and 48 recorded in the 4° squares near Eswatini, which represented only 29.6% or 22.5% endemism. Thus, endemism clearly increases greatly to the SW but is comparatively low in the hot central basin of the Botswana Kalahari and towards the N borders of the three countries (Figures 7C, 10D, 10E).

This trend in endemism is, presumably, related to the climatic and ecological conditions recorded within the map panel. The uplands (Figure 7A) and cold west coastal sea currents create cooler conditions than in the central Kalahari Basin and the tropical regions to the north (Figure 7C). The cold west coastal sea currents are also responsible for drier conditions and changing rainfall seasonality to the SW (Figures 7B, 7D) where winter rainfall replaces the summer rainfall experienced to the NE. These factors create unique regional and local ecological conditions, which have, presumably, driven speciation and high endemism with geographical barriers across the hot sands of the Botswana Kalahari and the hot, mostly dry Limpopo Valley in the NE.

This hypothesis is supported by the summary (Table 2) of geographical and climatic associations for endemic and non-endemic species (Appendix 1). Table 2 shows that average annual temperatures range from 15.71 to 16.77°C in the five most southwesterly patterns of distribution shown by endemic species (E1–E5). This reflects their spatial restriction by cool southern African temperatures (Figure 7B). The other five patterns shown by endemic species (E6–E10) have a more northeasterly bias with warmer average annual temperatures (18.43 to 19.52°C). Nevertheless, these remain lower than those in putative geographical barrier regions (>20°C) (Figure 7B). For non-endemic species, average annual temperatures for three patterns (17.15 to 19.71°C) are also lower than 20°C (NE1–NE3). However, these patterns comprise relatively few species that show distributions extending just over the Namibian border into S Angola (SW Arid; N Namibia = arid, savanna and psammophilous species combined), or on highlands in Zimbabwe and/or E Africa (Highveld). In the remaining four lowland patterns shown by non-endemic species (NE4–NE7), average annual temperatures

Table 2. Average data for different patterns of distribution shown by non-endemic and endemic species of dung beetles in South Africa, Botswana and Namibia (see also summary of distribution patterns for each species in Appendix 3)

Endemic patterns centred on:	Number of species, subsp.	Average climatic and topographical data			Average EOO (km²)
		Annual temperature (°C)	Annual rainfall (mm)	Altitude (m)	
E1. SW Cape	65	16.77	240	317	29 839
E2. S Cape	22	16.14	432	492	15 776
E3. Upper Karoo	10	16.03	318	1 206	254 724
E4. Highveld	88	15.68	708	1 345	110 292
E5. SW Arid – S Namib	20	16.44	114	992	11 858
E6. N Namibia	11	19.52	347	1 202	67 067
E7. E & NE Coast	17	19.45	867	308	23 585
E8. Kalahari	20	19.51	319	1 055	393 283
E9. SW Arid	14	18.43	219	1 065	232 507
E10. E Savanna	22	19.33	640	970	77 635
Non-endemic patterns centred on:					
NE1. Highveld	11	17.15	751	1 028	1 232 819
NE2. N Namibia	21	19.71	458	1 022	520 357
NE3. NE Coast	34	21.95	805	178	324 560
NE4. Kalahari	23	20.18	429	994	1 289 828
NE5. SW Arid	8	18.50	223	1 030	648 278
NE6. E Savanna	102	20.47	669	781	1 232 115
NE7. Savanna (E & W)	55	20.40	585	861	2 542 927

Table 3. Threatened or potentially threatened species with IUCN threat categories*

SOUTH AFRICA SPECIES	IUCN
ATEUCHINI	
Frankenbergerius barratti (Waterhouse, 1876)	DD/VU
Frankenbergerius gomesi (Ferreira, 1954a)	DD/VU
Frankenbergerius nanus (Péringuey, 1888)	DD/EN
Frankenbergerius opacus Frolov & Scholtz, 2005	DD/CR
Sarophorus bidentatus Frolov & Scholtz, 2003a	DD/VU
Sarophorus carinatus Frolov & Scholtz, 2003a	DD/EN
Sarophorus diabolus Roets, 2017	DD/CR
Sarophorus frolovi Roets, 2017	DD/VU
Sarophorus latus Frolov & Scholtz, 2003a	DD/VU
Sarophorus punctatus Frolov & Scholtz, 2003a	EN
CANTHONINI (DELTOCHILINI)	
Aliuscanthoniola similaris Deschodt & Scholtz, 2008	EN
Aphengoecus clypeatus Péringuey, 1901	DD/CR
Aphengoecus multiserratus Scholtz & Howden, 1987	VU
Bohepilissus nitidus (Balthasar, 1965a)	VU
Byrrhidium ovale Harold, 1869a	DD/VU
Circellium bacchus (Fabricius, 1781)	VU
Dwesasilvasedis medinae Deschodt & Scholtz, 2008	VU
Endroedyolus paradoxus Scholtz & Howden, 1987	VU
Epirinus aquilus Medina & Scholtz, 2005	VU
Epirinus bentoi Ferreira, 1964a	VU
Epirinus comosus Péringuey, 1901	DD/NT
Epirinus convexus Scholtz & Howden, 1987	DD/VU
Epirinus davisi Scholtz & Howden, 1987	DD/VU
Epirinus granulatus Scholtz & Howden, 1987	VU
Epirinus hluhluwensis Medina & Scholtz, 2005	DD/VU
Epirinus minimus Medina & Scholtz, 2005	VU
Epirinus montanus Scholtz & Howden, 1987	DD/EN
Epirinus ngomae Medina & Scholtz, 2005	DD/VU
Epirinus pseudorugosus Medina & Scholtz, 2005	DD/VU
Epirinus punctatus Scholtz & Howden, 1987	DD/VU
Epirinus sebastiani Medina & Scholtz, 2005	DD/VU
Gyronotus carinatus Felsche, 1911	VU
Gyronotus glabrosus Scholtz & Howden, 1987	VU
Gyronotus perissinottoi Moretto, 2013	DD/VU
Nebulasilvius insularis Deschodt & Scholtz, 2008	VU
Nebulasilvius johani Deschodt & Scholtz, 2008	VU
Parvuhowdenius harrisoni Deschodt & Scholtz, 2008	DD/VU
Peckolus alpinus Howden & Scholtz, 1988	DD/EN
Peckolus parvus Scholtz & Howden, 1987	DD/EN

SOUTH AFRICA SPECIES	IUCN
CANTHONINI (DELTOCHILINI) (continued)	
Peckolus poenskopius Deschodt & Scholtz, 2008	DD/EN
Silvaphilus ouboisiensis Roets & Oberlander, 2010	VU
COPRINI	
Copris jacchus (Fabricius 1775)	NT
Copris sexdentatus Thunberg, 1818	EN
Copris sphaeropterus Harold, 1877b	EN
Copris victorini Boheman, 1857	DD/EN
Macroderes amplior Frolov & Scholtz, 2004	DD/VU
Macroderes arrowi Janssens, 1939a	DD/VU
Macroderes cornutus Frolov & Scholtz, 2004	DD/VU
Macroderes endroedyi Frolov & Scholtz, 2004	NT
Macroderes fornicatus Sharp, 1880	DD/EN
Macroderes foveatus Frolov & Scholtz, 2004	DD/VU
Macroderes greeni (Kirby, 1818)	DD/VU
Macroderes minutus Frolov & Scholtz, 2004	DD/EN
Macroderes namakwanus Frolov & Scholtz, 2004	DD/VU
Macroderes politulus Preudhomme de Borre, 1880	DD/VU
Macroderes undulatus Preudhomme de Borre, 1880	NT
Xinidium dewitzi (Harold, 1878)	DD/VU
ONITINI	
Anonychonitis freyi Janssens, 1950	NT
Gilletellus porculus (Boheman, 1857)	DD/CR
Kolbeellus ateuchoides (van Lansberge 1875b)	DD/EN
Tropidonitis paradoxus (Boheman, 1857)	VU
SCARABAEINI	
Kheper clericus (Boheman, 1857)	DD/VU
Kheper zurstrasseni Davis, 1986	DD/EN
Pachysoma aesculapius (Olivier, 1789)	VU
Pachysoma endroedyi (Harrison, Scholtz & Chown, 2003)	EN
Pachysoma glentoni (Harrison, Scholtz & Chown, 2003)	VU
Scarabaeus bornemisszai zur Strassen, 1980	NT
Scarabaeus hequisti zur Strassen, 1962	DD/NT
Scarabaeus karae Davis & Deschodt 2017	DD/EN
Scarabaeus piliventris zur Strassen, 1962	DD/VU
Scarabaeus schulzeae Ferreira, 1969	DD/VU
SISYPHINI	
Sisyphus neobornemisszanus Daniel & Davis, 2016	NT
Sisyphus perissinottoi Montreuil, 2015c	DD/VU

BOTSWANA SPECIES	
ONTHOPHAGINI	
Mimonthophagus limbibasis (d'Orbigny, 1905)	DD/NT

NAMIBIA SPECIES	
CANTHONINI	
Dicranocara deschodti Frolov & Scholtz, 2003b	VU
ONITINI	
Platyonitis bicuariensis Ferreira, 1976b	VU
SCARABAEINI	
Pachysoma schinzi Fairmaire, 1888	DD/VU

*All endemic to South Africa, Botswana and/or Namibia (including Eswatini and Lesotho) except *Mimonthophagus limbibasis* (also Zimbabwe), *Platyonitis bicuariensis* (also Angola), *Tropidonitis paradoxus*, *Scarabaeus bornemisszai* and *Sisyphus neobornemisszanus* (also S Mozambique).

exceed 20°C (20.18 to 22.00°C). It is also noteworthy that average EOO (Extent of Occurrence) is greater in non-endemics than in endemics (Table 2).

Of 275 (out of 281) recorded endemic species (Figures 10B, 10E, Table 1), a total of 72 are currently listed as facing threats or potential threats (Figures 10C, 10F, Table 3). More than half of these species have been described since 1985 (Table 3). Clearly, species showing ecological specialisation, restricted range and/or endemism to highly transformed regions face the greatest threats. Therefore, threatened species are primarily recorded from South Africa, which is the most transformed of the three focal countries. Spatial patterns 1–4 (from pg. 710) contain the most transformed habitats in South Africa together with some in pattern 7 (see Mucina & Rutherford 2006: page 731, Figure 16.5). Thus, species that are allotted IUCN threat categories are mostly those centred on or localised within those spatial patterns (Table 4). Distributions of these species largely coincide with the Fynbos and Succulent Karoo Biomes (patterns 1–2), Indian Ocean Coastal Belt Biome (pattern 4) or small forest patches along the E escarpment encompassed by the Grassland Biome (pattern 3) (Figures I3, 9C, 9F). The few threatened species in patterns 6–7 are probably related to loss of preferred dung types due to range contraction in particular indigenous herbivores. Habitat transformation in the Grassland Biome remains worrisome as regards the various South African Highveld endemics. Transformation in the NE savanna regions has an impact, but most savanna species are also distributed beyond the borders of South Africa. Transformation in the SW Arid and Kalahari Savanna regions remains limited. However, the effects of range contraction of indigenous mammals overlie all these effects of vegetation modification and are mostly poorly known.

Table 4. Number of threatened or potentially threatened endemic species per spatial pattern in South Africa, Botswana and Namibia

Spatial pattern	IUCN category							
	CR	EN	VU	NT	DD/CR	DD/EN	DD/VU	DD/NT
1. SW Cape		1	8	2	3	3	10	
2. S Cape		3	3	1		2	1	
3. Highveld			4			6	8	1
4. E coast		1	2	1			5	
5. Kalahari								
6. SW Arid			1			1	1	
7. Savanna					1		2	

For an alternative, less qualitative assessment of biogeographical patterns and conservation of dung beetles in southern Africa, see Davis & Scholtz (2020).

APPENDIX 1: Summary Table 1. Distributions of 484 scarabaeine dung beetle species across biomes of South Africa (Mucina & Rutherford 2006) represented by proportions of occupied 1/16th degree squares; data comprising 20% or greater of total records are highlighted in yellow; conservation status assessed using IUCN Red List categories (IUCN 2001) and frequency of records; putative ecological bias assessed from available published or unpublished data (see Field Survey section under Introduction); see Synthesis section for key to division of tribes into clades of related species

Tribes and species (Clades, see Figure 5)	% of 1/16th degree squares occupied in summer rainfall biomes						% in winter rainfall biomes			Total N 1/16th degree squares	Conservation status (low frequency)	Putative ecological bias		
	Nama Karoo	Kalahari Savanna	Grassland	East Savanna	Indian Ocean Coastal Belt	Albany Thicket	Fynbos	Succulent Karoo	Desert			Soil	Veg.	Food
Ateuchini (Clade 1)														
Coptorhina auspicata	0	8	4	85	4	0	0	0	0	26	LC	Ss	GW	F
Coptorhina excavata	0	13	75	13	0	0	0	0	0	8	DD	Ss	G	F
Coptorhina klugii	0	2	33	45	14	4	2	0	0	51	LC	?Gen	GW	F
Coptorhina nitidipennis	0	0	9	87	4	0	0	0	0	23	LC	?	?	?F
Delopleurus pullus	0	10	0	80	10	0	0	0	0	10	LC	?	?	?F
Frankenbergerius armatus	0	0	46	31	12	12	0	0	0	26	LC	?	F>G	?
Frankenbergerius barratti	0	0	100	0	0	0	0	0	0	7	DD (R)	?Fg	?FG	?
Frankenbergerius forcipatus	0	0	33	17	0	50	0	0	0	6	DD (R)	?	?F	?
Frankenbergerius gomesi	0	0	25	67	8	0	0	0	0	12	DD (U)	?	FT	?F
Frankenbergerius nanus	0	0	0	0	0	0	100	0	0	4	DD (R, RR)	?Ss	?S	?
Frankenbergerius nitidus	0	0	0	0	0	0	0	100	0	1	DD (R, RR)	?Sa	?S	?
Frankenbergerius opacus	0	0	0	0	0	0	100	0	0	1	DD (R, RR)	?Fg	?S	?
Sarophorus bidentatus	0	0	0	0	0	0	0	100	0	1	DD (R, RR)	?	?	?
Sarophorus carinatus	0	0	100	0	0	0	0	0	0	2	DD (R, RR)	?	?T	?
Sarophorus costatus	0	3	20	73	5	0	0	0	0	102	LC	Gen	T>W>G	O>M>R
Sarophorus diabolus	0	0	0	0	0	0	100	0	0	1	DD (R, RR)	?Fg	?T	?O
Sarophorus frolovi	0	0	100	0	0	0	0	0	0	1	DD (R, RR)	?	?F	?O
Sarophorus latus	0	0	25	75	0	0	0	0	0	4	DD (R)	?	?	?OC
Sarophorus punctatus	0	0	0	0	0	0	100	0	0	1	DD (R, RR)	?	?F	?
Sarophorus striatus	0	0	0	13	0	63	25	0	0	8	LC (RR)	?	?	?
Sarophorus tuberculatus	0	0	0	0	0	29	71	0	0	14	LC	Ss	TS	?R

Tribes and species (Clades, see Figure 5)	% of 1/16th degree squares occupied in summer rainfall biomes						% in winter rainfall biomes			Total N 1/16th degree squares	Conser-vation status (low frequency)	Putative ecological bias		
	Nama Karoo	Kalahari Savanna	Grassland	East Savanna	Indian Ocean Coastal Belt	Albany Thicket	Fynbos	Succulent Karoo	Desert			Soil	Veg.	Food
Canthonini (Clade 2)														
Odontoloma apiculum	0	0	0	0	0	100	0	0	0	1	DD (R, RR)	?	?T	?
Odontoloma dentinum	0	0	0	0	0	13	60	27	0	15	LC	Ss	G>S	?
Odontoloma disalatum	0	0	0	0	0	0	100	0	0	5	DD	?	?	?
Odontoloma doubei	0	0	83	0	0	0	17	0	0	6	DD	?	?Gen	?Gen
Odontoloma endroedyi	11	0	0	0	0	11	56	22	0	9	LC	?	?	?O
Odontoloma louwi	0	13	50	38	0	0	0	0	0	8	LC	FG>Ss	?Gen	?
Odontoloma obscurum	0	0	50	0	0	25	25	0	0	4	LC	?	?	?
Odontoloma pauxillum	0	0	0	80	20	0	0	0	0	5	LC	?Sa	?	?
Odontoloma peckorum	0	0	75	25	0	0	0	0	0	12	LC	?FG	?G	?
Odontoloma planatum	0	0	83	17	0	0	0	0	0	2	DD	?Sa	?	?
Odontoloma pusillum	0	0	0	0	0	0	100	0	0	4	LC	Sa>Ss	SG	?
Odontoloma pygidiale	3	0	6	0	0	0	68	24	0	34	LC	?	?	?
Odontoloma quadridens	0	0	0	100	0	0	0	0	0	2	DD	?Sa	?	?
Odontoloma sculpturatum	0	0	43	29	0	14	14	0	0	7	DD	?	?	?
Odontoloma spinicaudum	0	0	0	0	0	0	0	100	0	1	DD (R, RR)	?sa	?S	?
Aliuscanthoniola similaris	0	0	0	0	100	0	0	0	0	1	EN (R, RR)	?FG	F	?
Endroedyolus paradoxus	0	0	100	0	0	0	0	0	0	2	EN (R, RR)	?	F	?
Nebulasilvius insularis	0	0	0	100	0	0	0	0	0	1	VU (U, RR)	?	F	?
Nebulasilvius johani	0	0	100	0	0	0	0	0	0	1	VU (R, RR)	?	F	?
Outenikwanus tomentosus	0	0	0	0	0	0	100	0	0	1	DD (R, RR)	?	F	?
Parvuhowdenius harrisoni	0	0	100	0	0	0	0	0	0	1	DD (R, RR)	?	F	?

CONSERVATION STATUS: DD = Data Deficient; LC = Least Concern; NT = Near Threatened; VU = Vulnerable; EN = Endangered; CR = Critically Endangered
FREQUENCY: U = Uncommon; R = Rare; RR = Range Restricted; LLR = Localised in Large Range
SOIL: Sa = Sand; Ss = Sandy Soils (Sand, Sandy loam); FG = Finer Grained (Sandy loam, Sandy clay loam, Clay); Gen = Generalist; ? = unknown or uncertain; > = is greater than;.
VEG. (VEGETATION): G = Pasture/Grassland; S = Scrub, Shrubland; W = Open Woodland, Woodland; F = Forest; T = Shaded Thicket; Gen = Generalist; > = is greater than; ? = unknown or uncertain.
FOOD: O = Omnivore dung, R = Ruminant herbivore dung; M = Monogastric herbivore dung; C = Carrion; Mi = Millipedes; F = Fungus; DGen = Dung Generalist; Dpellets = Dung pellets; Hyrax = Hyrax middens; > = is greater than; ? = unknown or uncertain.

APPENDIX 1: Summary Table 1. Distributions of 484 scarabaeine dung beetle species across biomes of South Africa (Mucina & Rutherford 2006) represented by proportions of occupied 1/16th degree squares; data comprising 20% or greater of total records are highlighted in yellow; conservation status assessed using IUCN Red List categories (IUCN 2001) and frequency of records; putative ecological bias assessed from available published or unpublished data (see Field Survey section under Introduction); see Synthesis section for key to division of tribes into clades of related species (continued)

Tribes and species (Clades, see Figure 5)	% of 1/16th degree squares occupied in summer rainfall biomes						% in winter rainfall biomes			Total N 1/16th degree squares	Conservation status (low frequency)	Putative ecological bias		
	Nama Karoo	Kalahari Savanna	Grassland	East Savanna	Indian Ocean Coastal Belt	Albany Thicket	Fynbos	Succulent Karoo	Desert			Soil	Veg.	Food
Canthonini (Clade 2) (continued)														
Peckolus alpinus	0	0	100	0	0	0	0	0	0	1	DD (R, RR)	?	F	?
Peckolus parvus	0	0	100	0	0	0	0	0	0	1	DD (R, RR)	?	F	?
Peckolus poenskopius	0	0	100	0	0	0	0	0	0	2	DD (R, RR)	?	F	?
Silvaphilus oubosiensis	0	0	0	0	0	0	100	0	0	1	VU (R, RR)	?	F	?Gen
Byrrhidium convexum	0	0	0	0	0	0	0	33	67	3	DD (R, RR)	?Ss	?	?Hyrax
Byrrhidium ovale	0	0	0	0	0	0	0	100	0	5	DD (R, RR)	?FG	S	Dpellets
Dicranocara tatasensis	0	0	0	0	0	0	0	100	0	1	LC (R, RR)	?Ss	?S	?Hyrax
Canthonini (Clade 4)														
Circellium bacchus	0	0	0	0	0	39	61	0	0	18	VU	?Ss	SW	RM
Ateuchini (Clade 5)														
Pedaria barrei	0	0	0	100	0	0	0	0	0	6	DD	?Ss	?W	?
Pedaria cylindrica	0	0	0	93	7	0	0	0	0	15	LC	?Ss	?GW	?
Pedaria picea	0	17	13	53	15	2	0	0	0	47	LC	Sa	GW>T	O>R>M
Pedaria segregis	0	0	0	85	15	0	0	0	0	13	LC	Sa	G?W	?
Coprini (Clade 5)														
Copris amyntor	0	2	3	94	1	0	0	0	0	120	LC	FG	W>TG	M>OR
Copris anceus	0	0	0	0	0	0	86	14	0	21	LC	Sa	S	?
Copris antares	4	2	65	8	2	14	6	0	0	51	LC	?Ss	?G	?
Copris bootes	0	0	0	100	0	0	0	0	0	4	LC (LLR)	?Ss	W	M
Copris caelatus	0	0	85	15	0	0	0	0	0	34	LC	FG	G	?
Copris cambeforti	0	0	0	100	0	0	0	0	0	2	DD (R, RR)	?	?	?
Copris capensis	0	0	0	0	0	0	58	42	0	31	LC	Ss	GS	?
Copris cassius	0	82	4	13	0	0	0	0	0	45	LC	Sa	G>SW	M>RO
Copris cornifrons	4	96	0	0	0	0	0	0	0	25	LC (U)	Sa	GS	?

Tribes and species (Clades, see Figure 5)	% of 1/16th degree squares occupied in summer rainfall biomes						% in winter rainfall biomes			Total N 1/16th degree squares	Conser-vation status (low frequency)	Putative ecological bias		
	Nama Karoo	Kalahari Savanna	Grassland	East Savanna	Indian Ocean Coastal Belt	Albany Thicket	Fynbos	Succulent Karoo	Desert			Soil	Veg.	Food
Copris corniger	1	0	85	8	1	4	1	0	0	78	LC	?FG	?G	?
Copris crassus	0	0	88	0	0	0	13	0	0	8	LC (U, LLR)	?FG	?	?
Copris denticulatus	0	5	8	86	1	1	0	0	0	104	LC	?FG	?Gen	?
Copris elphenor	1	22	11	64	2	0	0	0	0	184	LC	Ss	GW	R>M>O
Copris evanidus	0	14	5	81	0	0	0	0	0	118	LC	?Ss>FG	GW	M>R
Copris fidius	0	0	19	35	15	4	27	0	0	78	LC	?	F	RO
Copris inhalatus	0	13	6	31	50	0	0	0	0	16	LC (U)	Sa	G	?
Copris jacchoides	2	0	88	10	0	0	0	0	0	42	LC	FG	G	?R
Copris jacchus	0	0	0	0	0	40	60	0	0	5	NT (U, LLR)	?FG	?	?
Copris macer	0	0	57	43	0	0	0	0	0	21	LC	?FG	?G	?R
Copris mesacanthus	0	0	20	80	0	0	0	0	0	92	LC	FG	W>G>T	?RM
Copris obesus	0	3	54	42	1	0	0	0	0	78	LC	?Ss	GW	?
Copris orion caffer	0	0	0	17	44	33	6	0	0	18	LC	?	?	?
Copris puncticollis	0	0	0	44	56	0	0	0	0	16	LC	Sa	G	?
Copris ritsemae	0	0	44	56	0	0	0	0	0	9	LC	?	G	?
Copris sexdentatus	0	0	0	0	0	33	67	0	0	3	EN (R, RR)	?FG	?S	?
Copris sphaeropterus	0	0	0	0	0	0	100	0	0	1	EN (R, RR)	?	?	?
Copris urus	0	0	0	36	64	0	0	0	0	14	LC (RR)	Sa	GW	?
Copris victorini	0	0	0	0	0	0	100	0	0	4	DD (U, RR)	?Ss	?S	?
Copris vilhenai	0	0	0	100	0	0	0	0	0	23	LC	Ss	TW>G	M>R
Copris vrydaghi	0	0	75	25	0	0	0	0	0	4	DD	?	?	?
Litocopris muticus	0	0	0	100	0	0	0	0	0	2	LC	?FG	?FT	?M
Litocopris simplex	0	0	41	9	9	21	21	0	0	34	LC	?FG	?G	?
Canthonini (Clade 7)														
Gyronotus carinatus	0	0	0	20	80	0	0	0	0	5	VU (RR)	?	F	?

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Tribes and species (Clades, see Figure 5)	% of 1/16th degree squares occupied in summer rainfall biomes						% in winter rainfall biomes			Total N 1/16th degree squares	Conservation status (low frequency)	Putative ecological bias		
	Nama Karoo	Kalahari Savanna	Grassland	East Savanna	Indian Ocean Coastal Belt	Albany Thicket	Fynbos	Succulent Karoo	Desert			Soil	Veg.	Food
Canthonini (Clade 7) (continued)														
Gyronotus glabrosus	0	0	80	20	0	0	0	0	0	5	VU (RR)	?	G	?
Gyronotus perissinottoi	0	0	0	0	100	0	0	0	0	1	DD (RR)	?	G	?
Gyrontus pumilus	0	0	0	15	69	15	0	0	0	13	LC	?FG	F	?
Gyronotus schueli	0	0	50	50	0	0	0	0	0	2	DD (R, RR)	?	?G	?
Canthonini (Clade 10)														
Bohepilissus nitidus	0	0	0	0	0	0	100	0	0	1	VU (RR)	?	F	?
Bohepilissus subtilis	0	0	0	7	0	0	93	0	0	14	LC	?	F	?
Coprini (Clade 13)														
Catharsius aegeus	0	3	6	91	0	0	0	0	0	35	LC	?	?	C
Catharsius calaharicus	17	64	0	19	0	0	0	0	0	53	LC	Sa	GSW	OM>R
Catharsius harpagus	0	0	0	40	60	0	0	0	0	5	DD (RR)	Sa	G	?O
Catharsius heros	0	50	0	50	0	0	0	0	0	12	LC (LLR)	Ss	W	M>O
Catharsius laticeps	0	0	0	100	0	0	0	0	0	3	DD	?	?	?
Catharsius longiceps	0	0	75	25	0	0	0	0	0	8	DD	?	G	?
Catharsius marcellus	0	0	94	6	0	0	0	0	0	32	LC	?FG	G	?
Catharsius melancholicus	0	93	0	7	0	0	0	0	0	14	LC	Sa	?	C>O
Catharsius pandion	0	0	0	19	81	0	0	0	0	21	LC	Sa	FT	?
Catharsius philus	0	0	7	93	0	0	0	0	0	60	LC	FG	?	RO>M
Catharsius platycerus	0	0	0	100	0	0	0	0	0	1	DD (U, LLR)	?	?W	M
Catharsius sesostris	0	0	30	64	6	0	0	0	0	50	LC	?	T>W>G	OC>MR
Catharsius tricornutus	0	7	29	43	5	2	14	0	0	114	LC	Ss	W>GT	O>MR
Catharsius ulysses	0	40	15	45	0	0	0	0	0	40	LC	Ss	?WS>G	?
Catharsius vitulus	50	0	50	0	0	0	0	0	0	26	LC	Ss	GS	?
Metacatharsius anderseni	0	100	0	0	0	0	0	0	0	17	LC	Sa	?SG	M>OR
M. dentinum & zuluanus	36	32	2	22	8	0	0	0	0	50	LC	?Sa	?S	C>O>MR
Metacatharsius exiguiformis	25	75	0	0	0	0	0	0	0	53	LC	Sa	SG	Dgen
Metacatharsius exiguus	0	35	0	41	24	0	0	0	0	17	LC	Sa	SG	?RM
Metacatharsius ferreirae	0	0	0	100	0	0	0	0	0	1	DD	?Sa	?S	?C
Metacatharsius freyi	0	0	0	100	0	0	0	0	0	3	DD	?Sa	?	?
Metacatharsius latifrons	2	54	4	0	0	0	17	23	0	48	LC	Sa	SG	?OM>R

Tribes and species (Clades, see Figure 5)	% of 1/16th degree squares occupied in summer rainfall biomes						% in winter rainfall biomes			Total N 1/16th degree squares	Conser-vation status (low frequency)	Putative ecological bias		
	Nama Karoo	Kalahari Savanna	Grassland	East Savanna	Indian Ocean Coastal Belt	Albany Thicket	Fynbos	Succulent Karoo	Desert			Soil	Veg.	Food
Metacatharsius marani	72	26	1	0	0	0	0	1	0	90	LC	Ss	?S>G	?
M. opacus & *pseudoopacus*	2	4	4	78	12	0	0	0	0	51	LC	Ss	WS	CDGen
M. pumilionis & *pumilioni-formis*	0	62	3	35	0	0	0	0	0	37	LC	?	?	?
Metacatharsius troglodytes	0	29	4	68	0	0	0	0	0	77	LC	Sa	G	M>O>R
Coprini (Clade 14)														
Heliocopris andersoni	0	11	16	64	7	2	0	0	0	44	LC	?	?	?M>O
Heliocopris atropos	6	28	0	67	0	0	0	0	0	18	LC	Ss	WG	?M>RO
Heliocopris faunus	55	0	7	38	0	0	0	0	0	29	LC	?Gen	?WS	?
Heliocopris hamadryas	1	9	26	48	7	4	5	0	0	92	LC	?Ss	?	?
Heliocopris japetus	0	24	0	75	2	0	0	0	0	55	LC	Sa	?W>G	OM>R
Heliocopris neptunus	0	0	4	96	0	0	0	0	0	54	LC	?FG	GSW	?
Heliocopris pirmal	0	6	32	62	0	0	0	0	0	50	LC	?FG	?	?
Canthonini (Clade 16)														
Chalconotus convexus	0	1	6	82	10	1	0	0	0	136	LC	Gen	T>W>G	OC>M>R
Canthonini (Clade 18)														
Epirinus aeneus	41	6	0	0	0	1	39	10	3	80	LC	Ss	G>S	?
Epirinus aquilus	0	0	0	0	0	100	0	0	0	2	VU (R, RR)	Sa	F	?
Epirinus asper	0	0	73	27	0	0	0	0	0	15	LC	?FG	G	?
Epirinus bentoi	0	0	0	0	0	0	71	29	0	7	VU (U, RR)	Sa	S>G	?
Epirinus comosus	0	0	0	0	0	0	100	0	0	10	DD	Sa	S	?
Epirinus convexus	0	0	25	25	50	0	0	0	0	4	DD (R, RR)	?	F	?
Epirinus davisi	0	0	0	100	0	0	0	0	0	2	DD (R, RR)	?	F	?
Epirinus drakomontanus	0	0	100	0	0	0	0	0	0	2	DD (R, RR)	?FG	G	?

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FOOD: O = Omnivore dung, R = Ruminant herbivore dung; M = Monogastric herbivore dung; C = Carrion; Mi = Millipedes; F = Fungus; DGen = Dung Generalist; Dpellets = Dung pellets; Hyrax = Hyrax middens; > = is greater than; ? = unknown or uncertain.

APPENDIX 1: Summary Table 1. Distributions of 484 scarabaeine dung beetle species across biomes of South Africa (Mucina & Rutherford 2006) represented by proportions of occupied 1/16th degree squares; data comprising 20% or greater of total records are highlighted in yellow; conservation status assessed using IUCN Red List categories (IUCN 2001) and frequency of records; putative ecological bias assessed from available published or unpublished data (see Field Survey section under Introduction); see Synthesis section for key to division of tribes into clades of related species (continued)

Tribes and species (Clades, see Figure 5)	% of 1/16th degree squares occupied in summer rainfall biomes						% in winter rainfall biomes			Total N 1/16th degree squares	Conservation status (low frequency)	Putative ecological bias		
	Nama Karoo	Kalahari Savanna	Grassland	East Savanna	Indian Ocean Coastal Belt	Albany Thicket	Fynbos	Succulent Karoo	Desert			Soil	Veg.	Food
Canthonini (Clade 18) (continued)														
Epirinus flagellatus	4	0	7	0	0	4	55	29	0	69	LC	Ss	GS	?
Epirinus granulatus	0	0	0	0	0	0	50	50	0	8	VU (RR)	Sa	S	?
Epirinus gratus	0	53	47	0	0	0	0	0	0	17	LC	?	G	?
Epirinus hilaris	0	0	0	0	0	15	85	0	0	13	LC	?	SF	?
Epirinus hluhluwensis	0	0	0	100	0	0	0	0	0	1	DD (R, RR)	?	F	?
Epirinus minimus	0	0	0	0	0	50	50	0	0	2	VU (R, RR)	?	F	?
Epirinus montanus	0	0	0	0	0	0	100	0	0	3	DD (R, RR)	?	S	?
Epirinus mucrodentatus	0	0	50	50	0	0	0	0	0	2	DD (R, RR)	?	?	?
Epirinus ngomae	0	0	0	100	0	0	0	0	0	1	DD (RR)	?	F	?
Epirinus obtusus	18	0	45	5	0	27	5	0	0	22	LC	?FG	GS	?
Epirinus pseudorugosus	0	0	0	0	0	0	100	0	0	2	DD (R, RR)	Sa	G>S	?
Epirinus punctatus	0	0	80	20	0	0	0	0	0	5	DD (R)	?	F	?
Epirinus pygidialis	0	0	100	0	0	0	0	0	0	3	DD (R)	?	?FS	?
Epirinus relictus	0	0	44	11	0	0	44	0	0	9	LC (U)	?	?	?
Epirinus rugosus	0	0	0	0	0	0	100	0	0	1	DD (R, RR)	?	?	?
Epirinus scrobiculatus	0	0	0	0	0	0	41	59	0	17	LC	Sa	S>G	?
Epirinus sebastiani	0	0	100	0	0	0	0	0	0	1	DD (R, RR)	?	F	?
Epirinus silvestris	0	0	0	0	0	0	100	0	0	8	LC (U, RR)	?	F	?
Epirinus striatus	77	3	16	0	0	0	3	0	0	31	LC	Ss	?	?
Epirinus sulcipennis	0	0	0	0	0	0	100	0	0	1	DD (R, RR)	?Ss	?S	?
Epirinus validus	0	0	86	10	0	5	0	0	0	21	LC	?Ss	G	?
Canthonini (Clade 19)														
Aphengoecus clypeatus	0	0	0	0	0	0	100	0	0	1	DD (R, RR)	?	?	?

Tribes and species (Clades, see Figure 5)	% of 1/16th degree squares occupied in summer rainfall biomes						% in winter rainfall biomes			Total N 1/16th degree squares	Conser-vation status (low frequency)	Putative ecological bias		
	Nama Karoo	Kalahari Savanna	Grassland	East Savanna	Indian Ocean Coastal Belt	Albany Thicket	Fynbos	Succulent Karoo	Desert			Soil	Veg.	Food
Aphengoecus multserratus	0	0	0	0	0	0	88	13	0	8	VU (U, RR)	Sa	S	?
Canthonini (Clade 20)														
Dwesasilvasedis medinae	0	0	0	0	100	0	0	0	0	1	VU (R, RR)	?Ss	F	?
Pycnopanelus krikkeni	68	32	0	0	0	0	0	0	0	34	LC	Ss	?S>G	?
Coprini (Clade 21)														
Macroderes amplior	0	0	0	0	0	0	0	100	0	3	DD (R, RR)	?Ss	?S	?
Macroderes arrowi	0	0	0	0	0	0	0	100	0	1	DD (R, RR)	?Sa	?S	?
Macroderes bias	13	0	38	0	0	25	25	0	0	8	DD (U)	?Ss	?S	?
Macroderes cornutus	0	0	0	0	0	0	0	100	0	4	DD (R, RR)	?Sa	?S	?
Macroderes endroedyi	0	0	0	0	0	0	71	29	0	7	NT (R, RR)	?	?	?
Macroderes fornicatus	0	0	0	0	0	0	100	0	0	2	DD (R, RR)	Sa	S	?
Macroderes foveatus	0	0	0	0	0	0	50	50	0	4	DD (R, RR)	?	?	?
Macroderes greeni	0	0	0	0	0	0	100	0	0	3	DD (R, RR)	Sa	S	?
Macroderes minutus	0	0	0	0	0	0	22	78	0	9	DD R, RR)	?	?	?
Macroderes mutilans	0	0	0	0	0	0	0	100	0	4	DD (R, RR)	?	?	?
Macroderes namakwanus	0	0	0	0	0	0	0	100	0	4	DD (R, RR)	Sa	?	?
Macroderes nitidus	0	0	0	0	0	0	0	100	0	1	DD (R, RR)	?	?	?
Macroderes politulus	0	0	0	0	0	0	100	0	0	6	DD (R, RR)	?	?	?

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Tribes and species (Clades, see Figure 5)	% of 1/16th degree squares occupied in summer rainfall biomes						% in winter rainfall biomes			Total N 1/16th degree squares	Conservation status (low frequency)	Putative ecological bias		
	Nama Karoo	Kalahari Savanna	Grassland	East Savanna	Indian Ocean Coastal Belt	Albany Thicket	Fynbos	Succulent Karoo	Desert			Soil	Veg.	Food
Coprini (Clade 21) (continued)														
Macroderes undulatus	0	0	0	0	0	0	100	0	0	4	NT (R, RR)	?FG	?	?
Xinidium dentilabris	0	0	75	24	1	0	0	0	0	68	LC	FG	G	?
Xinidium dewitzi	0	0	75	25	0	0	0	0	0	4	DD (U, RR)	?	F	?
Xinidium howdeni	0	0	100	0	0	0	0	0	0	2	DD (R, RR)	?	F	?
Gymnopleurini (Clade 15)														
Allogymnopleurus consocius	0	0	44	56	0	0	0	0	0	9	DD (LLR)	FG	?	?R
Allogymnopleurus splendidus	21	19	9	47	3	0	0	0	0	180	LC	Ss	G>W	O>R>M
Garreta australugens	0	0	0	100	0	0	0	0	0	4	DD (U)	?FG	?	?
Garreta caffer	0	0	0	18	82	0	0	0	0	11	LC	Sa	F	?
Garreta laetus	0	0	50	50	0	0	0	0	0	2	LC	?	F	?
Garreta unicolor	0	0	41	50	9	0	0	0	0	74	LC	?FG	G>S>W	O>R>M
Garreta wahlbergi	0	0	5	94	1	0	0	0	0	102	LC	FG	W>T>G	O>R>M
Gymnopleurus aenescens	20	34	0	46	0	0	0	0	0	59	LC	Ss	GS>W	O>R>M
Gymnopleurus andreaei	76	24	0	0	0	0	0	0	0	50	LC	?Ss	GS	?DGen
Gymnopleurus asperrimus	65	35	0	0	0	0	0	0	0	71	LC	?Ss	GS	?DGen
Gymnopleurus humanus	71	21	5	0	0	2	1	1	0	111	LC	?Ss	GS	?DGen
Gymnopleurus humeralis	0	0	0	100	0	0	0	0	0	67	LC	?Ss	SW	O>R
Gymnopleurus leei	23	0	63	0	0	2	13	0	0	48	LC	?Gen	G	?
Gymnopleurus pumilus	0	0	0	100	0	0	0	0	0	66	LC	FG	?W	O>R>M
Gymnopleurus reichei	0	0	0	100	0	0	0	0	0	4	LC (R, LLR)	?	?	?Gen
Gymnopleurus thelwalli	0	0	0	100	0	0	0	0	0	4	DD (R)	?	?	?
Gymnopleurus virens	0	0	33	64	3	0	0	0	0	66	LC	FG	W>G>T	?
Oniticellini (Clade 23)														
Afrodrepanus impressicollis	0	0	10	67	24	0	0	0	0	21	LC	?FG>Ss	FW	O>R>M
Cyptochirus ambiguus	0	0	56	30	3	2	8	0	0	86	LC	FG	G	?R
Drepanocerus kirbyi	0	1	36	48	4	8	3	0	0	75	LC	Gen	WT>G	R>M>O
Drepanocerus patrizii	14	14	22	44	0	6	0	0	0	36	LC	Gen	W>G>T	RM

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	Nama Karoo	Kalahari Savanna	Grassland	East Savanna	Indian Ocean Coastal Belt	Albany Thicket	Fynbos	Succulent Karoo	Desert			Soil	Veg.	Food
Eodrepanus bechynei	0	0	0	100	0	0	0	0	0	4	LC	?Gen	?	?RM
Eodrepanus fastiditus	0	2	30	61	7	0	0	0	0	44	LC	FG>Sa	GW	M>R
Eodrepanus parallelus	0	0	0	100	0	0	0	0	0	2	LC	?	?	?RM
Epidrepanus pulvinarius/ caelatus	0	0	40	55	5	0	0	0	0	20	DD	?FG	W	DGen
Euoniticellus africanus	15	6	55	5	1	5	11	1	0	149	LC	?FG	G	?RM
Euoniticellus intermedius	19	13	19	33	3	4	9	1	0	281	LC	Gen	WG>T	R>M>O
Euonticellus kawanus	0	0	0	100	0	0	0	0	0	1	DD (U, LLR)	?	?W	M
Euoniticellus triangulatus	1	0	40	25	5	5	24	1	0	128	LC	?Gen	G	?RM
Euoniticellus zumpti	0	0	0	93	7	0	0	0	0	14	DD	?	?W	M>O
Ixodina abyssinica	0	0	0	100	0	0	0	0	0	4	DD	?	?	?RM
Latodrepanus laticollis	0	3	0	97	0	0	0	0	0	33	LC	Sa>FG	W>G>T	RM>O
Liatongus militaris	1	3	31	50	7	3	6	0	0	184	LC	FG>Sa	G>W>T	M>R
Oniticellus egregius	0	0	4	92	4	0	0	0	0	25	LC (U)	?	?	M
Oniticellus formosus	2	16	7	68	7	0	0	0	0	57	LC	FG>Sa	G>W>T	M>R
Oniticellus pictus	0	0	42	13	0	19	26	0	0	31	LC	?FG	?G>W	?RM
Oniticellus planatus	0	0	29	47	8	6	10	0	0	113	LC	Gen	?G>W>T	?MR
Paraixodina freyi	0	0	0	86	14	0	0	0	0	7	DD (LLR)	?FG	?W	?M
Paraixodina saegeri	0	0	0	100	0	0	0	0	0	6	DD (LLR)	?	?WF	M
Tibiodrepanus sulcicollis	0	0	52	17	7	7	17	0	0	29	LC	?FG	?G	?MR
Tiniocellus eurypygus	0	0	6	94	0	0	0	0	0	50	LC	Sa>FG	W>GT	M>O>R
Tiniocellus spinipes	0	0	0	100	0	0	0	0	0	10	LC	?FG	?W	?M
Tragiscus dimidiatus	0	0	0	100	0	0	0	0	0	13	LC (U, LLR)	?Gen	?W	M
Onitini (Clade 22)														
Anonychonitis freyi	0	0	0	100	0	0	0	0	0	2	NT (R, RR)	?	?	M
Cheironitis audens	86	14	0	0	0	0	0	0	0	49	LC	Gen	SW	MR

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	Nama Karoo	Kalahari Savanna	Grassland	East Savanna	Indian Ocean Coastal Belt	Albany Thicket	Fynbos	Succulent Karoo	Desert			Soil	Veg.	Food
Onitini (Clade 22) (continued)														
Cheirontis hoplosternus	36	31	20	10	0	0	3	0	0	80	LC	Ss	SW	MR
Cheironitis imitator	0	0	0	100	0	0	0	0	0	11	DD	Ss	W	M
Cheironitis indicus	79	21	0	0	0	0	0	0	0	28	LC	Ss	SW	MR
Cheironitis scabrosus	57	14	5	0	0	0	14	10	0	107	LC	Gen	G	R
Heteronitis castelnaui	0	0	0	97	3	0	0	0	0	36	LC	FG	W	M
Kolbeellus ateuchoides	50	0	50	0	0	0	0	0	0	2	DD (R, RR)	?	?	?M
Megalonitis bohemani	0	0	0	100	0	0	0	0	0	1	DD (R, LLR)	?Gen	?W	M
Neonitis nigritiae	0	0	0	100	0	0	0	0	0	1	DD (R)	?	?	M
Onitis aeruginosus	0	0	0	100	0	0	0	0	0	2	LC	?Ss	W	MO
Onitis alexis	5	11	27	49	2	3	3	0	0	248	LC	Gen	G>W>T	RM
Onitis aygulus	28	18	19	0	0	5	25	5	0	111	LC	Gen	GS	R
Onitis caffer	5	7	38	25	2	5	17	2	0	210	LC	Gen	G	R
Onitis confusus	17	17	4	0	0	9	43	9	0	23	LC	Sa	SG	RM
Onitis cribratus	0	0	100	0	0	0	0	0	0	3	DD (R, RR)	FG	G	?R
Onitis curvipes	15	8	38	0	0	0	31	8	0	13	DD (R)	?FG	G	?M
Onitis deceptor	0	40	0	50	10	0	0	0	0	30	LC	Sa	W>T>G	?MR
Onitis fabricii	0	0	8	92	0	0	0	0	0	12	LC	FG	GW	RM
Onitis fulgidus	0	0	7	93	0	0	0	0	0	70	LC	FG	TW	O>M>R
Onitis inversidens	0	0	0	100	0	0	0	0	0	13	LC (LLR)	FG	WT	M
Onitis licitus	0	0	100	0	0	0	0	0	0	2	DD (R)	?FG	?G	?
Onitis longitibialis	100	0	0	0	0	0	0	0	0	1	DD (R)	?	?S	?M
Onitis mendax	0	0	0	100	0	0	0	0	0	22	LC (LLR)	FG	W	M
Onitis minutus	0	0	0	0	0	9	82	9	0	11	DD	?Ss	GS	?R
Onitis obenbergeri	0	0	0	100	0	0	0	0	0	14	LC	Ss	W	M>O>R
Onitis paraconfusus	0	0	0	100	0	0	0	0	0	2	DD (R, RR)	Sa	W	M
Onitis parainflaticollis	0	27	9	45	18	0	0	0	0	11	DD (R)	?	?	?

Tribes and species (Clades, see Figure 5)	% of 1/16th degree squares occupied in summer rainfall biomes						% in winter rainfall biomes			Total N 1/16th degree squares	Conser-vation status (low frequency)	Putative ecological bias		
	Nama Karoo	Kalahari Savanna	Grassland	East Savanna	Indian Ocean Coastal Belt	Albany Thicket	Fynbos	Succulent Karoo	Desert			Soil	Veg.	Food
Onitis pecuarius	0	0	47	21	6	6	19	0	0	78	LC	FG	G	R
Onitis perpunctatus	0	0	51	43	0	2	4	0	0	47	LC	FG	F>G	RO
Onitis picticollis	0	0	20	78	3	0	0	0	0	40	LC	Gen	GW	M
Onitis pseudosetosus	0	0	0	100	0	0	0	0	0	12	LC	Ss	W	?MO
Onitis robustus	0	0	0	100	0	0	0	0	0	2	LC (U, LLR)	FG	W	M
Onitis tortuosus	0	1	64	29	5	1	1	0	0	133	LC	FG	G	R
Onitis uncinatus	1	13	13	71	1	0	0	0	0	134	LC	FG	W>G>T	RM
Onitis viridulus	0	1	10	84	5	0	0	0	0	92	LC	FG	Gen	MR
Onitis westermanni	0	0	0	100	0	0	0	0	0	6	LC	Gen	GW	?R
Tropidonitis paradoxus	0	0	0	67	33	0	0	0	0	3	VU (RR)	Sa	?WF	M
Onthophagini (Clade 23)														
Caccobiomorphus megaponerae	0	0	0	100	0	0	0	0	0	3	LC (R)	?	?	?Ant prey
Caccobius castaneus	0	0	0	100	0	0	0	0	0	5	DD (U)	?Gen	?	?RM
Caccobius cavatus	0	8	0	42	50	0	0	0	0	12	LC	Sa	?	O>MR
Caccobius ferrugineus	0	30	2	67	0	0	0	0	0	46	LC	Sa	G>WT	O>M>R
Caccobius histerinus	0	0	0	80	20	0	0	0	0	25	LC	Sa	?	?
Caccobius nigritulus	2	9	0	83	6	0	0	0	0	47	LC	Sa	W>T>G	O>M>R
Caccobius obtusus	0	0	55	22	5	0	17	0	0	58	LC	?FG	?G	?
Cleptocaccobius convexifrons	0	0	0	100	0	0	0	0	0	4	LC	Sa	WG>T	O>R>M
Cleptocaccobius postlutatus	0	0	35	58	8	0	0	0	0	26	LC	?	?	?
Cleptocaccobius viridicollis	9	20	13	52	6	0	0	0	0	64	LC	FG>Sa	W>G>T	O>R>M
Digitonthophagus gazella	4	9	16	56	4	5	7	0	0	221	LC	FG>Sa	G>W>T	?
Digitonthophagus namaquensis	48	30	0	0	0	4	4	13	0	23	LC	?	?	?
Euonthophagus carbonarius	0	0	3	95	2	0	0	0	0	63	LC	?	?	?
Euonthophagus flavimargo	19	81	0	0	0	0	0	0	0	47	LC	?Ss	?W	O>M>R
Euonthophagus jeanneli	0	0	0	100	0	0	0	0	0	12	LC	Sa	GS	OM>R
Euonthophagus vicarius	83	0	6	0	0	3	6	3	0	36	LC	?Gen	?S	?

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SOIL: Sa = Sand; Ss = Sandy Soils (Sand, Sandy loam); FG = Finer Grained (Sandy loam, Sandy clay loam, Clay); Gen = Generalist; ? = unknown or uncertain; > = is greater than;.

VEG. (VEGETATION): G = Pasture/Grassland; S = Scrub, Shrubland; W = Open Woodland, Woodland; F = Forest; T = Shaded Thicket; Gen = Generalist; > = is greater than; ? = unknown or uncertain.

FOOD: O = Omnivore dung, R = Ruminant herbivore dung; M = Monogastric herbivore dung; C = Carrion; Mi = Millipedes; F = Fungus; DGen = Dung Generalist; Dpellets = Dung pellets; Hyrax = Hyrax middens; > = is greater than; ? = unknown or uncertain.

APPENDIX 1: Summary Table 1. Distributions of 484 scarabaeine dung beetle species across biomes of South Africa (Mucina & Rutherford 2006) represented by proportions of occupied 1/16th degree squares; data comprising 20% or greater of total records are highlighted in yellow; conservation status assessed using IUCN Red List categories (IUCN 2001) and frequency of records; putative ecological bias assessed from available published or unpublished data (see Field Survey section under Introduction); see Synthesis section for key to division of tribes into clades of related species (continued)

Tribes and species (Clades, see Figure 5)	% of 1/16th degree squares occupied in summer rainfall biomes						% in winter rainfall biomes			Total N 1/16th degree squares	Conservation status (low frequency)	Putative ecological bias		
	Nama Karoo	Kalahari Savanna	Grassland	East Savanna	Indian Ocean Coastal Belt	Albany Thicket	Fynbos	Succulent Karoo	Desert			Soil	Veg.	Food
Onthophagini (Clade 23) (continued)														
Hamonthophagus acutus	29	71	0	0	0	0	0	0	0	21	LC	?Sa	?S	?
Hamonthophagus depressus	1	0	9	73	18	0	0	0	0	80	LC	?Ss	?W	?
Haroldius convexus	0	0	0	100	0	0	0	0	0	1	DD (R)	?	?	?Ant prey
Heteroclitopus remipes	0	20	0	60	20	0	0	0	0	5	DD (R)	?	?	?Termites
Hyalonthophagus alcyon	0	0	0	100	0	0	0	0	0	1	DD	?Sa	?W	?M>R
Hyalonthophagus alcyonides	0	0	12	83	5	0	0	0	0	42	LC	?Gen	W>G>T	O>MR
Kurtops caffrarius	-	-	-	-	-	-	-	-	-	0	DD (R)	?	?	?
Kurtops quadraticeps	9	79	0	12	0	0	0	0	0	34	LC	Sa	SG	O>M>R
Kurtops signatus	30	32	0	33	5	0	0	0	0	106	LC	Sa	W>G	O>M>R
Milichus apicalis	0	0	0	100	0	0	0	0	0	17	LC (LLR)	FG	?W	M
Mimonthophagus ambiguus	0	0	0	20	80	0	0	0	0	10	LC	Sa	G>F	?
Mimonthophagus anomalus	0	0	0	100	0	0	0	0	0	3	LC (LLR)	?	?	O>M>R
Onthophagus absyrtus	0	0	91	9	0	0	0	0	0	11	DD	?FG	?G	?
Onthophagus aequepubens	0	0	0	100	0	0	0	0	0	12	LC	?	T	?
Onthophagus aeruginosus	1	0	27	67	5	0	0	0	0	113	LC	Gen	WT>G	O>MR
Onthophagus albipennis	91	2	2	0	0	2	2	0	0	44	LC	Gen	?GS	?
Onthophagus albipodex	0	0	6	94	0	0	0	0	0	16	LC	?Sa>FG	G>SW	?
Onthophagus apiciosus	0	0	20	80	0	0	0	0	0	20	LC	?	?	?C
Onthophagus asperulus	0	0	67	24	5	5	0	0	0	88	LC	?FG	?G	?
Onthophagus beiranus	0	0	0	76	24	0	0	0	0	21	LC	FG	WT	?RM
Onthophagus bicavifrons	1	6	11	74	8	0	0	0	0	87	LC	?	?	C
Onthophagus binodis	1	0	62	15	2	3	17	0	0	115	LC	?FG	?G	?R
Onthophagus bovinus	24	24	6	47	0	0	0	0	0	17	LC	?	?	?
Onthophagus cameloides	21	0	0	0	0	3	51	25	0	71	LC	?Ss	G	?RM
Onthophagus cinctipennis	0	5	59	27	9	0	0	0	0	22	LC	?Sa, Ss	G>W>T	?
Onthophagus cineraceus	0	0	0	0	0	0	100	0	0	2	DD (R, RR)	?	?	?
Onthophagus convexus	47	38	0	15	0	0	0	0	0	68	LC	?Sa, Ss	G>W	O>M>R
Onthophagus corniculiger	0	0	0	100	0	0	0	0	0	12	DD (U, LLR)	?	?	M

Tribes and species (Clades, see Figure 5)	% of 1/16th degree squares occupied in summer rainfall biomes						% in winter rainfall biomes			Total N 1/16th degree squares	Conser-vation status (low frequency)	Putative ecological bias		
	Nama Karoo	Kalahari Savanna	Grassland	East Savanna	Indian Ocean Coastal Belt	Albany Thicket	Fynbos	Succulent Karoo	Desert			Soil	Veg.	Food
Onthophagus cretus	0	0	14	57	29	0	0	0	0	14	LC	?	F	?
Onthophagus cribripennis	0	1	43	44	8	2	1	0	0	84	LC	?FG	?GF	O>R
Onthophagus croesulus	0	0	27	73	0	0	0	0	0	11	DD	?	?	C
Onthophagus cupricollis	0	0	20	80	0	0	0	0	0	10	DD	?	?	C
Onthophagus cyaneoniger	7	7	68	14	0	0	4	0	0	28	LC	Ss	G	?
O. deterrens & *variolosus*	0	2	47	30	5	0	16	0	0	57	DD	?FG	?G	C
Onthophagus discretus	0	0	10	90	0	0	0	0	0	10	LC	FG>Sa	T	?
Onthophagus ebenicolor	0	0	3	88	10	0	0	0	0	40	LC	?FG	?W	?C
Onthophagus ebenus	0	1	26	64	9	0	0	0	0	70	LC	FG>Sa	GW	OC
Onthophagus fimetarius	0	2	29	67	2	0	0	0	0	96	LC	?Ss>FG	Gen	O>RM
Onthophagus flavolimbatus	0	5	2	83	10	0	0	0	0	42	LC	Ss>FG	GW	OR>M
Onthophagus fritschi	43	2	47	0	0	5	0	3	0	58	LC	?Gen	GS	?
Onthophagus fugitivus	0	0	19	81	0	0	0	0	0	16	DD	?FG	?SW	?
Onthophagus giraffa	0	0	0	0	0	3	97	0	0	34	LC	?Ss	G>S	?
O. giuseppecarpenetoi	0	0	0	56	44	0	0	0	0	9	LC (RR)	Sa	G>F	?M
Onthophagus granulifer	19	73	4	4	0	0	0	0	0	48	LC	Ss	?GW	O>M>R
Onthophagus graphicus	0	33	0	67	0	0	0	0	0	6	DD	?	?	C
Onthophagus herus	0	0	0	100	0	0	0	0	0	2	LC (LLR)	?	?TF	?OC
Onthophagus hyaena	0	0	73	0	0	0	27	0	0	30	LC	?FG	?G	?
Onthophagus immundus	0	0	0	0	0	0	90	10	0	10	LC	?Ss	?G	?
Onthophagus interstitialis	1	0	59	38	1	0	0	0	0	68	LC	FG>Ss	G>W	O>RM
Onthophagus juvencus	0	0	0	38	63	0	0	0	0	8	LC	Sa	G	?
Onthophagus lacustris	0	0	0	40	60	0	0	0	0	10	LC	?Sa	FT	?O>R
Onthophagus lamelliger	0	0	0	100	0	0	0	0	0	49	LC	?Gen	?W	O>M>R
Onthophagus lamnifer	0	0	100	0	0	0	0	0	0	27	LC	?FG	?G	?R
Onthophagus leroyi	0	0	0	100	0	0	0	0	0	20	LC	?FG	?WFT	?
Onthophagus leucopygus	9	70	17	4	0	0	0	0	0	23	LC	?Ss	?GSW	?DGen

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FOOD: O = Omnivore dung, R = Ruminant herbivore dung; M = Monogastric herbivore dung; C = Carrion; Mi = Millipedes; F = Fungus; DGen = Dung Generalist; Dpellets = Dung pellets; Hyrax = Hyrax middens; > = is greater than; ? = unknown or uncertain.

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Tribes and species (Clades, see Figure 5)	% of 1/16th degree squares occupied in summer rainfall biomes						% in winter rainfall biomes			Total N 1/16th degree squares	Conservation status (low frequency)	Putative ecological bias		
	Nama Karoo	Kalahari Savanna	Grassland	East Savanna	Indian Ocean Coastal Belt	Albany Thicket	Fynbos	Succulent Karoo	Desert			Soil	Veg.	Food
Onthophagini (Clade 23) (continued)														
Onthophagus lugubris	0	0	80	10	0	5	5	0	0	40	LC	?FG	?G	?
Onthophagus minutus	0	0	0	0	0	3	90	7	0	30	LC	Sa	GS	?
Onthophagus monodon	0	0	100	0	0	0	0	0	0	10	LC	?	?	?
Onthophagus naso	0	0	31	38	25	6	0	0	0	16	LC	?FG	?G	?OC
Onthophagus obtusicornis	1	11	25	54	6	0	2	1	0	100	LC	?Gen	G>W>T	CO>M>R
Onthophagus obtutus	0	0	100	0	0	0	0	0	0	28	LC	FG	G	?
Onthophagus pallidipennis	0	22	4	72	2	0	0	0	0	50	LC	Ss>FG	W>G>T	RO>M
Onthophagus parumnotatus	0	0	45	49	6	0	0	0	0	53	LC	FG	G	O>R>M
Onthophagus pauxillus	0	2	13	83	2	0	0	0	0	46	LC	?Gen	W>G>T	RO>M
Onthophagus pellax	0	13	7	80	0	0	0	0	0	15	LC	Ss	?G>W	?
Onthophagus peringueyi	84	3	5	0	0	5	2	0	0	58	LC	?Gen	GS	?
Onthophagus pilosus	0	0	65	24	6	0	6	0	0	34	LC	Ss	?G>W	?
Onthophagus plebejus	0	0	0	88	13	0	0	0	0	8	LC (LLR)	?Ss	?W	O>M (M)
Onthophagus probus	58	42	0	0	0	0	0	0	0	71	LC	Ss	GS	O>MR
Onthophagus producticollis	0	0	13	87	0	0	0	0	0	15	DD	FG	WT	?
Onthophagus pugionatus	4	1	23	60	11	0	0	0	0	73	LC	Ss>FG	T>W>G	?O>RM
Onthophagus pullus	0	0	7	89	4	0	0	0	0	27	LC	Sa	T>W>G	?O
Onthophagus quadrimaculatus	0	13	6	63	19	0	0	0	0	16	DD	?FG>Ss	T	?C
Onthophagus quadrinodosus	0	3	9	76	12	0	0	0	0	34	LC	Sa	TW>G	O>RM
Onthophagus rasipennis	0	0	4	94	2	0	0	0	0	47	LC	?FG or Ss	W>TG	?DGen
Onthophagus scapularis	0	0	0	0	0	100	0	0	0	2	DD	?	?	?C
Onthophagus semiflavus	36	64	0	0	0	0	0	0	0	39	LC	?Ss	GS	O>MR
Onthophagus suffusus	0	0	0	100	0	0	0	0	0	11	LC	?Ss	?W	O>M>R
Onthophagus trinodosus	0	0	0	100	0	0	0	0	0	12	DD (U)	?FG	?S	?O>R
Onthophagus ursinus	0	0	0	22	78	0	0	0	0	9	LC	?Sa	?WG	?
Onthophagus venustulus	18	63	3	16	0	0	0	0	0	67	LC	Ss	?WS>G	OM>R
Onthophagus verticalis	4	31	0	65	0	0	0	0	0	26	LC	Ss	TW>G	MO>R
Onthophagus vigens	0	0	67	23	3	7	0	0	0	30	LC	FG	G	?
Onthophagus vinctus	2	6	11	69	12	1	0	0	0	147	LC	Ss	T>W>G	O>MR
Onthophagus virescens	0	0	0	100	0	0	0	0	0	4	LC	Sa	?W	O>M>R

Tribes and species (Clades, see Figure 5)	% of 1/16th degree squares occupied in summer rainfall biomes						% in winter rainfall biomes			Total N 1/16th degree squares	Conser-vation status (low frequency)	Putative ecological bias		
	Nama Karoo	Kalahari Savanna	Grassland	East Savanna	Indian Ocean Coastal Belt	Albany Thicket	Fynbos	Succulent Karoo	Desert			Soil	Veg.	Food
Onthophagus vylderi	0	0	0	100	0	0	0	0	0	3	LC	Sa	?W	C
Phalops ardea	0	0	0	100	0	0	0	0	0	47	LC	?Ss	?W	O>RM
Phalops boschas	0	0	0	100	0	0	0	0	0	57	LC	?Ss	?W	O>RM
Phalops bubalus	19	1	61	5	0	13	0	0	0	77	LC	?Gen	?G	?R
Phalops dregei	37	15	11	34	0	3	0	0	0	100	LC	?Gen	GW	O>RM
Phalops flavocinctus	0	1	15	81	3	0	0	0	0	78	LC	FG	G>W	O>MR
Phalops pryroides	80	20	0	0	0	0	0	0	0	20	LC	Ss	?SW	?
Phalops rufosignatus	28	53	6	0	0	11	3	0	0	36	LC	?Gen	?GW	O>M>R
Phalops smaragdinus	0	0	4	89	7	0	0	0	0	46	LC	?Ss	W>G	O>MR
Phalops wittei	33	45	11	12	0	0	0	0	0	103	LC	Sa	GS>W	O>M>R
Proagoderus aciculatus	0	0	0	40	52	8	0	0	0	25	LC	Sa	F	?O>RM
Proagoderus aureiceps	0	0	0	62	38	0	0	0	0	29	LC	Sa	G	?
Proagoderus bicallosus	0	0	0	81	19	0	0	0	0	21	LC (LLR)	Ss	W	MO
Proagoderus chalcostolus	0	0	40	45	15	0	0	0	0	73	LC	FG	G	?
Proagoderus dives	0	0	0	78	22	0	0	0	0	18	LC	Sa	FW	?O>MR
Proagoderus furcifer	0	0	0	100	0	0	0	0	0	1	DD (R, LLR)	?Ss	?SW	M
Proagoderus lanista	10	0	68	12	8	2	0	0	0	50	LC	FG	G	?
Proagoderus loricatus	0	0	3	97	0	0	0	0	0	29	LC (LLR)	?Ss	?SW	O>MR (M)
Proagoderus quadrituber	0	0	17	67	17	0	0	0	0	6	LC	FG	WF	?
Proagoderus rangifer	0	0	0	100	0	0	0	0	0	17	LC (LLR)	?Ss	SW	O>MR (M)
Proagoderus rectefurcatus	0	0	0	100	0	0	0	0	0	6	LC (LLR)	?Ss	SW	M
Proagoderus sapphirinus	0	52	4	44	0	0	0	0	0	48	LC	Sa	GW>T	O>CMR
Proagoderus tersidorsis	0	0	2	94	4	0	0	0	0	50	LC	FG	?W	?
Scarabaeini (Clade 4)														
Escarabaeus satyrus	55	22	3	6	0	1	3	8	1	119	LC	Ss	GS	?RM

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Tribes and species (Clades, see Figure 5)	% of 1/16th degree squares occupied in summer rainfall biomes						% in winter rainfall biomes			Total N 1/16th degree squares	Conservation status (low frequency)	Putative ecological bias		
	Nama Karoo	Kalahari Savanna	Grassland	East Savanna	Indian Ocean Coastal Belt	Albany Thicket	Fynbos	Succulent Karoo	Desert			Soil	Veg.	Food
Scarabaeini (Clade 4) (continued)														
Kheper bonellii	0	0	0	0	0	0	54	46	0	24	LC	Ss	SG	?RM
Kheper clericus	0	0	0	100	0	0	0	0	0	4	DD (RR)	FG	W	MR
Kheper cupreus	0	0	0	100	0	0	0	0	0	25	LC	Ss	SW	OR
Kheper kalaharicus	0	100	0	0	0	0	0	0	0	2	LC (RR)	Sa	GS	OR
Kheper lamarcki	0	32	3	54	11	0	0	0	0	65	LC	Sa	W>GT	O>MR>C
Kheper nigroaeneus	0	3	9	88	0	0	0	0	0	103	LC	Gen	WG	O>R>M
Kheper prodigiosus	0	25	0	75	0	0	0	0	0	20	LC	Sa	G>W	M>O>R
Kheper subaeneus	0	0	14	86	0	0	0	0	0	44	LC	FG	WG	O>MR
Kheper zurstrasseni	0	0	33	67	0	0	0	0	0	3	DD (R, RR)	?	?	?
Pachylomera femoralis	0	16	6	65	13	0	0	0	0	68	LC	Sa	GW	O>CMR
Pachylomera opacus	21	74	0	5	0	0	0	0	0	43	LC	Sa	GS	O>MR
Pachysoma aesculapius	0	0	0	0	0	0	100	0	0	15	VU (RR)	Sa	S	Rpellets
Pachysoma bennigseni	0	0	0	0	0	0	0	75	25	4	LC (RR)	Sa	?S	Detritus
Pachysoma endroedyi	0	0	0	0	0	0	0	100	0	1	EN (R, RR)	Sa	S	Detritus
Pachysoma gariepinum	0	0	0	0	0	0	0	92	8	12	LC	Sa	?S	Detritus
Pachysoma glentoni	0	0	0	0	0	0	100	0	0	3	VU (R, RR)	Sa	S	Detritus
Pachysoma hippocrates	0	0	0	0	0	0	34	66	0	29	LC (RR)	Sa	S	Detritus
Pachysoma striatum	0	0	0	0	0	0	0	100	0	23	LC (RR)	Sa	S	Rpellets
Scarabaeolus anderseni	7	85	0	7	0	0	0	0	0	27	LC	Sa	SG	C
Scarabaeolus andreaei	0	0	0	100	0	0	0	0	0	1	LC	Sa	?S	?O
Scarabaeolus bohemani	50	11	16	21	0	0	1	0	0	123	LC	Gen	GS	CO>MR
Scarabaeolus carniphilus	0	100	0	0	0	0	0	0	0	1	DD	Sa	G	C>R
Scarabaeolus clanceyi	0	0	0	100	0	0	0	0	0	6	LC	Sa	G	O
Scarabaeolus damarensis	12	86	0	2	0	0	0	0	0	42	LC	Sa	GS	OR>M
Scarabaeolus flavicornis	23	47	5	5	0	0	3	15	3	75	LC	Sa	G	OC>MR
Scarabaeolus fritschi	79	0	0	0	0	0	0	18	3	34	LC	Sa	GS	?
Scarabaeolus gracai	0	0	0	100	0	0	0	0	0	2	DD (RR)	Sa	?	?
Scarabaeolus inoportunus	27	70	3	0	0	0	0	0	0	33	LC	Sa	GS	DGenC
Scarabaeolus inquisitus	22	44	11	22	0	0	0	0	0	18	LC	Sa	GS	C>dung

Tribes and species (Clades, see Figure 5)	% of 1/16th degree squares occupied in summer rainfall biomes						% in winter rainfall biomes			Total N 1/16th degree squares	Conser-vation status (low frequency)	Putative ecological bias		
	Nama Karoo	Kalahari Savanna	Grassland	East Savanna	Indian Ocean Coastal Belt	Albany Thicket	Fynbos	Succulent Karoo	Desert			Soil	Veg.	Food
Scarabaeolus intricatus	0	0	0	0	0	0	68	33	0	40	LC	Ss	S>G	?
Scarabaeolus karrooensis	86	14	0	0	0	0	0	0	0	21	LC	?	?	?
Scarabaeolus kochi	35	65	0	0	0	0	0	0	0	26	LC	Sa	GS	CO>MR
Scarabaeolus lucidulus	0	0	0	100	0	0	0	0	0	2	DD	Sa	?W	Banana-CO
Scarabaeolus megaparvulus	100	0	0	0	0	0	0	0	0	18	LC	?Gen	?SG	?
Scarabaeolus niemandi	0	0	0	100	0	0	0	0	0	4	DD (RR)	?Sa	?W	?
Scarabaeolus pabulator	81	5	0	5	0	0	0	5	5	21	LC	Sa	S	?
Scarabaeolus parvulus	50	46	0	0	0	0	0	2	2	46	LC	Sa	SG	?DGen
Scarabaeolus planipennis	0	0	0	80	20	0	0	0	0	5	LC (RR)	Sa	GW>F	?O
Scarabaeolus reichei	0	0	0	0	0	0	46	54	0	24	LC	Ss	GS	?C+dung
Scarabaeolus rubripennis	0	0	0	0	0	0	0	75	25	4	LC	Sa	?	?
Scarabaeolus soutpansbergensis	0	0	0	100	0	0	0	0	0	7	DD (RR)	?Sa	?SW	?
Scarabaeus alienus	0	0	0	0	0	0	0	100	0	2	DD (R)	Ss	S	?M
Scarabaeus ambiguus	7	26	35	32	0	0	0	0	0	57	LC	?Ss	G	?
Scarabaeus basuto	43	0	57	0	0	0	0	0	0	42	LC	?FG	G	?R
Scarabaeus bornemisszai	0	0	0	0	100	0	0	0	0	10	NT (RR)	Sa	F	?O
Scarabaeus caffer	0	0	45	50	5	0	0	0	0	22	LC	FG	G	OR
Scarabaeus spretus & convexus	0	0	36	9	5	5	41	5	0	22	DD	?	?	?
Scarabaeus costatus	29	65	3	0	0	0	0	3	0	31	LC	Sa	GS	O>R
Scarabaeus deludens	0	3	9	88	0	0	0	0	0	32	LC	FG	SW	MR
Scarabaeus ebenus	0	0	0	82	18	0	0	0	0	11	LC (U)	Sa	W	O
Scarabaeus funebris	13	13	40	33	0	0	0	0	0	15	DD (U)	FG	GSW	?
Scarabaeus galenus	0	0	3	97	0	0	0	0	0	30	LC	Ss	W	?Rpellets
Scarabaeus geminogalenus	0	0	0	77	23	0	0	0	0	13	LC	Sa	G	?
Scarabaeus goryi	0	15	6	65	15	0	0	0	0	62	LC	Sa	Gen	O>RM
Scarabaeus heqvisti	0	0	33	67	0	0	0	0	0	3	DD (RR)	Sa	G	?
Scarabaeus hottentorum	0	0	0	0	0	0	0	100	0	5	DD (RR)	Ss	S	OR

CONSERVATION STATUS: DD = Data Deficient; LC = Least Concern; NT = Near Threatened; VU = Vulnerable; EN = Endangered; CR = Critically Endangered

FREQUENCY: U = Uncommon; R = Rare; RR = Range Restricted; LLR = Localised in Large Range

SOIL: Sa = Sand; Ss = Sandy Soils (Sand, Sandy loam); FG = Finer Grained (Sandy loam, Sandy clay loam, Clay); Gen = Generalist; ? = unknown or uncertain; > = is greater than;.

VEG. (VEGETATION): G = Pasture/Grassland; S = Scrub, Shrubland; W = Open Woodland, Woodland; F = Forest; T = Shaded Thicket; Gen = Generalist; > = is greater than; ? = unknown or uncertain.

FOOD: O = Omnivore dung, R = Ruminant herbivore dung; M = Monogastric herbivore dung; C = Carrion; Mi = Millipedes; F = Fungus; DGen = Dung Generalist; Dpellets = Dung pellets; Hyrax = Hyrax middens; > = is greater than; ? = unknown or uncertain.

APPENDIX 1: Summary Table 1. Distributions of 484 scarabaeine dung beetle species across biomes of South Africa (Mucina & Rutherford 2006) represented by proportions of occupied 1/16th degree squares; data comprising 20% or greater of total records are highlighted in yellow; conservation status assessed using IUCN Red List categories (IUCN 2001) and frequency of records; putative ecological bias assessed from available published or unpublished data (see Field Survey section under Introduction); see Synthesis section for key to division of tribes into clades of related species (continued)

Tribes and species (Clades, see Figure 5)	% of 1/16th degree squares occupied in summer rainfall biomes						% in winter rainfall biomes			Total N 1/16th degree squares	Conservation status (low frequency)	Putative ecological bias		
	Nama Karoo	Kalahari Savanna	Grassland	East Savanna	Indian Ocean Coastal Belt	Albany Thicket	Fynbos	Succulent Karoo	Desert			Soil	Veg.	Food
Scarabaeini (Clade 4) (continued)														
Scarabaeus interstitialis	0	13	13	73	0	0	0	0	0	15	LC (U)	?	GW	?
Scarabaeus karae	0	0	100	0	0	0	0	0	0	3	DD (R, RR)	?	G	?
Scarabaeus piliventris	0	0	0	0	0	0	40	60	0	5	DD (U, RR)	?Ss	GS	?
Scarabaeus proboscideus	25	37	0	0	0	0	14	22	2	81	LC	Sa	?S	?DGen
Scarabaeus proximus	0	0	0	0	0	0	0	90	10	10	LC	Sa	S	?
Scarabaeus rixosus	-	-	-	-	-	-	-	-	-	0	DD (R, RR)	?	?	?
Scarabaeus rugosus	0	0	0	0	0	0	55	45	0	33	LC	Sa	S	?
Scarabaeus rusticus	0	2	26	72	0	0	0	0	0	85	LC	?Gen	W	?
Scarabaeus savignyi	0	0	0	0	0	33	67	0	0	6	DD (U)	?FG	?S	?
Scarabaeus schulzae	0	0	0	100	0	0	0	0	0	8	DD (RR)	?	?WF	?
Scarabaeus suri	0	0	0	0	0	0	83	17	0	23	LC	Ss	SG	?RM
Scarabaeus viator	81	6	4	0	0	4	3	1	0	67	LC	Gen	GS	?
Scarabaeus vicinus	52	33	2	12	0	0	0	0	0	42	LC	Sa	GS	?Rpellets
Scarabaeus westwoodi	0	0	100	0	0	0	0	0	0	6	LC	FG	G	?R
Scarabaeus zambesianus	0	33	0	67	0	0	0	0	0	33	LC	Sa	SW	DGen
Sceliages adamastor	20	0	30	0	0	10	30	10	0	10	DD	?	?S	Mi
Sceliages brittoni	0	0	0	0	0	0	42	58	0	12	LC	Sa	S	Mi
Sceliages difficilis	0	0	29	71	0	0	0	0	0	24	LC	?Sa	?GS	?Mi
Sceliages gagates	0	0	0	50	50	0	0	0	0	4	LC	Sa	?G	?Mi
Sceliages granulatus	25	75	0	0	0	0	0	0	0	4	LC	Sa	GS	Mi
Sceliages hippias	0	0	19	81	0	0	0	0	0	31	LC	?	?SW	Mi
Sisyphini (Clade 18)														
Neosisyphus barbarossa	0	0	83	0	0	6	11	0	0	18	LC	?FG	G	?R
Neosisyphus calcaratus	0	0	6	92	2	0	0	0	0	50	LC	Ss> FG	SW	R>O>M
Neosisyphus confrater	0	0	38	33	29	0	0	0	0	24	LC	FG, Ss	G	?
Neosisyphus fortuitus	0	0	10	78	12	0	0	0	0	41	LC	?Gen	T>W>G	?
Neosisyphus infuscatus	0	0	12	70	12	6	0	0	0	33	LC	FG, Ss	?W>GF	R>OM

Tribes and species (Clades, see Figure 5)	% of 1/16th degree squares occupied in summer rainfall biomes						% in winter rainfall biomes			Total N 1/16th degree squares	Conser-vation status (low frequency)	Putative ecological bias		
	Nama Karoo	Kalahari Savanna	Grassland	East Savanna	Indian Ocean Coastal Belt	Albany Thicket	Fynbos	Succulent Karoo	Desert			Soil	Veg.	Food
Neosisyphus kuehni	0	0	100	0	0	0	0	0	0	7	DD (U)	?Gen	G	?R
Neosisyphus macrorubrus	32	35	31	2	0	0	0	0	0	65	LC	?Gen	?SG>W	?R
Neosisyphus mirabilis	0	0	0	36	45	9	9	0	0	11	LC	Ss>FG	FT	?
Neosisyphus quadricollis	17	0	0	0	0	0	83	0	0	6	DD	?	?	?
Neosisyphus rubrus	0	5	38	50	3	3	1	0	0	172	LC	FG>Ss	G>W>T	R>MO
Neosisyphus spinipes	0	0	7	63	20	3	7	0	0	71	LC	Gen	?G>W>T	?R>MO
Sisyphus caffer	0	2	75	17	5	0	2	0	0	59	LC	?FG	G	OR>M
Sisyphus costatus	0	0	82	15	3	0	0	0	0	34	LC	FG	G	O>R>M
Sisyphus fasciculatus	0	0	17	75	8	0	0	0	0	24	LC	FG	FT>W	OR>M
Sisyphus goryi	0	2	9	86	1	0	1	0	0	85	LC	Gen	W>GT	OR>M
Sisyphus impressipennis	0	0	3	97	0	0	0	0	0	31	LC	?Ss	TF	?O>RM
Sisyphus manni	0	0	41	54	5	0	0	0	0	37	LC	?Ss	GW	?
Sisyphus muricatus	0	0	61	4	0	0	35	0	0	23	LC	?FG	G	?
Sisyphus nanniscus	0	0	2	77	21	0	0	0	0	43	LC	Gen,Ss>FG	T	O>R>M
Sisyphus neobornemisszanus	0	0	0	0	100	0	0	0	0	5	NT (LLR)	Sa	F	?
Sisyphus oralensis	0	0	0	42	58	0	0	0	0	12	LC	Sa	FT	?
Sisyphus perissinottoi	0	0	0	0	0	67	33	0	0	3	DD	?	?	?
Sisyphus sordidus	0	0	0	62	38	0	0	0	0	29	LC	Sa	G	?
Sisyphus umbraphilus	0	0	0	100	0	0	0	0	0	4	DD	?Sa	T	O>R
Total numbers of species	**108**	**148**	**241**	**320**	**153**	**86**	**130**	**71**	**12**	**484**				

CONSERVATION STATUS: DD = Data Deficient; LC = Least Concern; NT = Near Threatened; VU = Vulnerable; EN = Endangered; CR = Critically Endangered
FREQUENCY: U = Uncommon; R = Rare; RR = Range Restricted; LLR = Localised in Large Range
SOIL: Sa = Sand; Ss = Sandy Soils (Sand, Sandy loam); FG = Finer Grained (Sandy loam, Sandy clay loam, Clay); Gen = Generalist; ? = unknown or uncertain; > = is greater than;.
VEG. (VEGETATION): G = Pasture/Grassland; S = Scrub, Shrubland; W = Open Woodland, Woodland; F = Forest; T = Shaded Thicket; Gen = Generalist; > = is greater than; ? = unknown or uncertain.
FOOD: O = Omnivore dung, R = Ruminant herbivore dung; M = Monogastric herbivore dung; C = Carrion; Mi = Millipedes; F = Fungus; DGen = Dung Generalist; Dpellets = Dung pellets; Hyrax = Hyrax middens; > = is greater than; ? = unknown or uncertain.

APPENDIX 2: Summary Table 2. Distributions of 217 scarabaeine dung beetle species across ecoregions of Namibia and Botswana (Olson et al. 2001) represented by proportions of occupied 1/16th degree squares; data comprising 20% or greater of total records are highlighted in yellow; conservation status assessed using IUCN Red List categories (IUCN 2001) and frequency of records; see Synthesis section for key to division of tribes into clades of related species

Tribes and species (clades, see Figure 5)	% of Arid Namibia & Botswana ecoregions (AT 13++)						% of Mesic Namibia & Botswana savanna ecoregions (AT07++)					Total N 1/16th degree squares	Conservation status (low frequency)
	Succulent Karoo	Nama Karoo	Namib Desert	Kaokoveld Desert	Namibian Savanna Woodlands	Kalahari Xeric Savanna	Kalahari Acacia Baikiaea Woodlands	Zambezian & Mopane Woodlands	Angolan Mopane Woodlands	Southern African Bushveld	Zambezian Baikiaea Woodlands		
Ateuchini (Clade 1)													
Coptorhina auspicata	0	0	0	0	0	67	0	33	0	0	0	6	LC
Coptorhina nitidipennis	0	0	0	0	0	33	67	0	0	0	0	3	LC
Delopleurus darrenmanni	0	0	0	0	0	0	0	100	0	0	0	2	DD
Delopleurus gilleti	0	0	0	0	100	0	0	0	0	0	0	1	LC
Delopleurus pullus	0	0	0	0	50	0	0	0	50	0	0	4	LC
Sarophorus angolensis	0	0	0	0	100	0	0	0	0	0	0	1	DD (RR)
Sarophorus costatus	0	0	0	0	0	50	0	0	0	50	0	2	LC
Canthonini (Clade 2)													
Dicranocara deschodti	0	100	0	0	0	0	0	0	0	0	0	2	VU (R, RR)
Dicranocara inexpectata	0	100	0	0	0	0	0	0	0	0	0	1	DD (R, RR)
Dicranocara vandersmisseni	0	100	0	0	0	0	0	0	0	0	0	2	DD (R,RR)
Drogo stalsi	0	100	0	0	0	0	0	0	0	0	0	1	DD (R, RR)
Namakwanus irishi	0	0	0	0	0	100	0	0	0	0	0	1	DD (R, RR)
Namakwanus scholtzi	0	0	100	0	0	0	0	0	0	0	0	1	DD (R, RR)
Namaphilus ameibensis	0	0	0	0	100	0	0	0	0	0	0	1	DD (R, RR)
Namaphilus davisi	0	0	0	0	0	100	0	0	0	0	0	1	DD (R, RR)
Namaphilus endroedyi	0	0	0	0	100	0	0	0	0	0	0	2	DD (R, RR)
Odontoloma louwi	0	0	0	0	56	22	11	0	11	0	0	9	LC
Versicorpus erongoensis	0	0	0	0	100	0	0	0	0	0	0	1	DD (R, RR)
Versicorpus streyi	0	0	0	0	100	0	0	0	0	0	0	1	DD (R, RR)
Ateuchini (Clade 5)													
Pedaria brancoi	0	0	0	0	0	50	0	0	0	0	50	2	DD
Pedaria cylindrica	0	0	0	0	0	0	50	0	0	0	50	2	LC
Pedaria picea	0	0	0	0	0	50	50	0	0	0	0	4	LC
Coprini (Clade 5)													
Copris amyntor	0	0	0	0	0	22	56	11	0	11	0	9	LC
Copris bootes	0	0	0	0	0	0	0	100	0	0	0	3	LC (LLR)
Copris cassius	0	0	0	0	0	85	15	0	0	0	0	20	LC

Tribes and species (clades, see Figure 5)	% of Arid Namibia & Botswana ecoregions (AT 13++)						% of Mesic Namibia & Botswana savanna ecoregions (AT07++)					Total N 1/16th degree squares	Conservation status (low frequency)
	Succulent Karoo	Nama Karoo	Namib Desert	Kaokoveld Desert	Namibian Savanna Woodlands	Kalahari Xeric Savanna	Kalahari Acacia Baikiaea Woodlands	Zambezian & Mopane Woodlands	Angolan Mopane Woodlands	Southern African Bushveld	Zambezian Baikiaea Woodlands		
Copris cornifrons	0	0	0	0	0	71	29	0	0	0	0	7	LC (U)
Copris denticulatus	0	0	0	0	0	0	75	0	0	25	0	4	LC
Copris elphenor	0	0	0	0	5	44	20	15	10	5	0	59	LC
Copris evanidus	0	0	0	0	0	7	57	0	0	36	0	14	LC
Copris gracilis	0	0	0	0	29	45	2	0	24	0	0	42	LC
Copris inhalatus	0	0	0	0	0	71	14	0	0	0	14	7	LC (U)
Copris laioides	0	0	0	0	0	40	13	0	47	0	0	15	LC
Copris mesacanthus	0	0	0	0	0	0	0	75	0	0	25	4	LC
Copris puncticollis	0	0	0	0	0	0	0	71	29	0	0	7	LC
Copris subsidens	0	0	0	0	40	33	0	0	26	0	0	42	LC
Copris vilhenai	0	0	0	0	0	0	0	80	0	20	0	5	LC
Coprini (Clade 13)													
Catharsius aegeus	0	0	0	0	0	0	29	43	0	14	14	7	LC
Catharsius calaharicus	0	0	0	0	6	62	24	6	3	0	0	34	LC
Catharsius heros	0	0	0	0	11	0	33	22	22	0	11	9	LC (LLR)
Catharsius melancholicus	0	0	0	0	17	50	17	8	0	0	8	12	LC
Catharsius philus	0	0	0	0	0	0	83	0	0	17	0	6	LC
Catharsius tricornutus	0	0	0	0	0	0	0	60	40	0	0	5	LC
Catharsius ulysses	0	0	0	0	13	58	17	0	13	0	0	24	LC
Metacatharsius anderseni	0	0	0	0	0	100	0	0	0	0	0	8	LC
Metacatharsius dentinum	0	0	4	0	32	43	11	7	0	0	4	28	LC
Metacatharsius exiguiformis	0	0	9	4	27	53	4	0	0	2	0	45	LC
Metacatharsius exiguus	0	0	0	0	0	82	9	0	9	0	0	11	LC
Metacatharsius ferreirae	0	0	0	0	0	25	50	25	0	0	0	4	DD
Metacatharsius freyi	0	0	0	0	0	25	75	0	0	0	0	4	DD
Metacatharsius latifrons	0	0	0	0	0	100	0	0	0	0	0	11	LC
Metacatharsius marani	0	0	4	0	28	60	0	0	8	0	0	25	LC
Metacatharsius opacus	0	0	0	0	10	31	25	17	12	2	4	52	LC
Metacatharsius pumilioni-formis	0	0	0	0	25	50	25	0	0	0	0	8	LC
Metacatharsius troglodytes	0	0	0	0	0	29	32	18	21	0	0	34	LC

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FREQUENCY: U = Uncommon; R = Rare; RR = Range Restricted; LLR = Localised in Large Range

APPENDIX 2: Summary Table 2. Distributions of 217 scarabaeine dung beetle species across ecoregions of Namibia and Botswana (Olson et al. 2001) represented by proportions of occupied 1/16th degree squares; data comprising 20% or greater of total records are highlighted in yellow; conservation status assessed using IUCN Red List categories (IUCN 2001) and frequency of records; see Synthesis section for key to division of tribes into clades of related species (continued)

Tribes and species (clades, see Figure 5)	% of Arid Namibia & Botswana ecoregions (AT 13++)						% of Mesic Namibia & Botswana savanna ecoregions (AT07++)					Total N 1/16th degree squares	Conservation status (low frequency)
	Succulent Karoo	Nama Karoo	Namib Desert	Kaokoveld Desert	Namibian Savanna Woodlands	Kalahari Xeric Savanna	Kalahari Acacia Baikiaea Woodlands	Zambezian & Mopane Woodlands	Angolan Mopane Woodlands	Southern African Bushveld	Zambezian Baikiaea Woodlands		
Coprini (Clade 14)													
Heliocopris andersoni	0	3	0	0	23	39	6	3	23	0	3	31	LC
Heliocopris atropos	0	0	0	0	6	63	6	13	6	0	6	16	LC
Heliocopris faunus	0	0	7	0	34	31	3	0	21	3	0	29	LC
Heliocopris hamadryas	0	0	0	0	0	50	0	50	0	0	0	2	LC
Heliocopris japetus	0	0	0	0	0	53	17	20	10	0	0	30	LC
Heliocopris neptunus	0	0	0	0	25	0	25	25	0	25	0	4	LC
Canthonini (Clade 16)													
Chalconotus convexus	0	0	2	0	37	14	5	16	14	7	5	43	LC
Canthonini (Clade 20)													
Hammondantus psammophilus	17	0	67	0	17	0	0	0	0	0	0	6	LC (R)
Pycnopanelus krikkeni	0	4	12	4	62	19	0	0	0	0	0	26	LC
Gymnopleurini (Clade 15)													
Allogymnopleurus splendidus	0	0	0	0	0	52	17	13	0	13	4	23	LC
Garreta nitens	0	0	0	0	28	17	17	0	39	0	0	18	LC
Garreta wahlbergi	0	0	0	0	0	0	0	0	0	67	33	3	LC
Gymnopleurus aenescens	0	0	4	4	34	28	14	10	2	2	2	50	LC
Gymnopleurus andreaei	0	8	21	4	58	8	0	0	0	0	0	24	LC
Gymnopleurus asperrimus	0	14	0	0	0	86	0	0	0	0	0	7	LC
Gymnopleurus humanus	0	4	13	5	54	20	0	0	5	0	0	80	LC
Gymnopleurus humeralis	0	0	0	0	0	0	0	0	0	100	0	1	LC
Gymnopleurus ignitus	0	0	0	0	0	0	13	50	0	25	13	8	LC
Gymnopleurus imitator	0	0	0	0	0	100	0	0	0	0	0	1	DD (R, RR)
Gymnopleurus pumilus	0	0	0	0	23	23	19	15	19	0	0	26	LC
Gymnopleurus virens	0	0	0	0	0	50	50	0	0	0	0	2	LC
Oniticellini (clade 23)													
Drepanocerus kirbyi	0	0	0	0	0	0	0	100	0	0	0	2	LC
Euoniticellus intermedius	3	3	3	0	21	42	8	5	11	3	3	38	LC
Euonticellus kawanus	0	0	0	0	33	0	0	33	33	0	0	6	DD (U, LLR)

Tribes and species (clades, see Figure 5)	% of Arid Namibia & Botswana ecoregions (AT 13++)						% of Mesic Namibia & Botswana savanna ecoregions (AT07++)					Total N 1/16th degree squares	Conservation status (low frequency)
	Succulent Karoo	Nama Karoo	Namib Desert	Kaokoveld Desert	Namibian Savanna Woodlands	Kalahari Xeric Savanna	Kalahari Acacia Baikiaea Woodlands	Zambezian & Mopane Woodlands	Angolan Mopane Woodlands	Southern African Bushveld	Zambezian Baikiaea Woodlands		
Euoniticellus triangulatus	0	0	0	0	0	0	0	0	0	0	100	1	LC
Latodrepanus laticollis	0	0	0	0	0	0	50	50	0	0	0	4	LC
Liatongus militaris	0	0	0	0	0	0	0	100	0	0	0	1	LC
Oniticellus egregius	0	0	0	0	20	0	20	0	60	0	0	5	LC (U)
Oniticellus formosus	0	0	0	0	0	0	50	50	0	0	0	2	LC
Oniticellus planatus	0	0	0	0	0	0	0	50	0	0	50	2	LC
Paraixodina saegeri	0	0	0	0	0	0	0	100	0	0	0	2	DD (LLR)
Tiniocellus spinipes	0	0	0	0	0	0	0	0	0	0	100	3	LC
Tragiscus dimidiatus	0	0	0	0	0	0	0	50	50	0	0	2	LC
Onitini (Clade 22)													
Cheironitis audens	0	0	0	0	14	0	0	0	86	0	0	7	LC
Cheirontis hoplosternus	0	0	0	0	0	20	20	0	60	0	0	5	LC
Cheironitis imitator	0	0	0	0	0	0	0	100	0	0	0	3	DD
Cheironitis indicus	0	20	40	0	40	0	0	0	0	0	0	5	LC
Cheironitis scabrosus	10	30	10	0	40	10	0	0	0	0	0	10	LC
Gilletellus porculus	0	0	0	0	0	0	0	0	100	0	0	1	DD (R, LLR)
Heteronitis castelnaui	0	0	0	0	15	0	8	15	46	0	15	13	LC
Megalonitis bohemani	0	0	0	0	0	0	25	25	25	0	25	4	DD (R, LLR)
Onitis aeruginosus	0	0	0	0	0	0	50	0	0	0	50	2	LC
Onitis alexis	0	0	0	0	23	28	20	14	11	2	2	64	LC
Onitis aygulus	0	50	0	0	0	50	0	0	0	0	0	4	LC
Onitis bilobatus	0	0	0	0	100	0	0	0	0	0	0	1	DD (R, RR)
Onitis caffer	0	0	0	0	0	100	0	0	0	0	0	2	LC
Onitis confusus	0	0	100	0	0	0	0	0	0	0	0	1	LC
Onitis deceptor	0	0	0	0	0	0	0	100	0	0	0	2	LC
Onitis fulgidus	0	0	0	0	0	0	0	57	0	29	14	7	LC
Onitis inversidens	0	0	0	0	0	0	0	100	0	0	0	2	LC (LLR)
Onitis mendax	0	0	0	0	0	0	0	0	80	0	20	5	LC (LLR)
Onitis mniszechi	0	0	20	0	20	40	0	0	20	0	0	5	DD
Onitis obenbergeri	0	0	0	0	0	0	0	100	0	0	0	1	LC
Onitis obscurus	0	0	0	0	24	12	18	0	47	0	0	17	LC

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APPENDIX 2: Summary Table 2. Distributions of 217 scarabaeine dung beetle species across ecoregions of Namibia and Botswana (Olson et al. 2001) represented by proportions of occupied 1/16th degree squares; data comprising 20% or greater of total records are highlighted in yellow; conservation status assessed using IUCN Red List categories (IUCN 2001) and frequency of records; see Synthesis section for key to division of tribes into clades of related species (continued)

Tribes and species (clades, see Figure 5)	% of Arid Namibia & Botswana ecoregions (AT 13++)						% of Mesic Namibia & Botswana savanna ecoregions (AT07++)					Total N 1/16th degree squares	Conservation status (low frequency)
	Succulent Karoo	Nama Karoo	Namib Desert	Kaokoveld Desert	Namibian Savanna Woodlands	Kalahari Xeric Savanna	Kalahari Acacia Baikiaea Woodlands	Zambezian & Mopane Woodlands	Angolan Mopane Woodlands	Southern African Bushveld	Zambezian Baikiaea Woodlands		
Onitini (Clade 22) (continued)													
Onitis orthopus	0	0	0	0	0	0	50	25	0	0	25	4	LC
Onitis parainflaticollis	0	0	0	0	0	100	0	0	0	0	0	1	DD (R)
Onitis picticollis	0	0	0	0	100	0	0	0	0	0	0	1	LC
Onitis robustus	0	0	0	0	0	0	25	50	25	0	0	4	LC (U, LLR)
Onitis setosus	0	0	0	0	57	0	0	0	43	0	0	7	LC
Onitis uncinatus	0	0	0	0	20	24	16	10	26	4	0	50	LC
Onitis viridulus	0	0	0	0	0	20	20	60	0	0	0	5	LC
Onitis westermanni	0	0	0	0	0	0	33	0	0	67	0	3	LC
Platyonitis bicuariensis	0	0	0	0	0	0	0	0	100	0	0	1	VU (R, LLR)
Onthophagini (Clade 23)													
Caccobius castaneus	0	0	0	0	40	0	20	0	20	0	20	5	DD (U)
Caccobius cavatus	0	0	0	0	0	20	20	40	0	0	20	5	LC
Caccobius ferrugineus	0	0	0	3	16	31	31	9	3	0	6	32	LC
Caccobius histerinus	0	0	0	0	0	0	0	100	0	0	0	2	LC
Caccobius nigritulus	0	0	0	0	0	45	18	27	0	0	9	11	LC
Cleptocaccobius convexifrons	0	0	0	0	0	33	33	0	0	0	33	3	LC
Cleptocaccobius viridicollis	0	0	3	0	67	13	10	0	3	0	3	30	LC
Digitonthophagus gazella	0	0	0	0	0	17	48	30	0	0	4	23	LC
Digitonthophagus namaquensis	0	6	10	0	65	13	0	0	6	0	0	31	LC
Digitonthophagus viridicollis	0	0	0	0	39	25	7	0	21	0	7	28	LC
Euonthophagus carbonarius	0	0	0	0	0	0	44	56	0	0	0	9	LC
Euonthophagus flavimargo	0	0	0	0	0	100	0	0	0	0	0	7	LC
Hamonthophagus acutus	0	11	22	0	28	33	6	0	0	0	0	18	LC
Hamonthophagus depressus	0	0	0	0	75	8	17	0	0	0	0	12	LC
Hamonthophagus fallax	0	0	0	0	0	0	0	40	0	0	60	5	DD
Hyalonthophagus alcyon	0	0	0	0	0	0	0	25	25	0	50	4	DD
Hyalonthophagus alcyonides	0	0	0	0	0	0	100	0	0	0	0	2	LC
Kurtops quadraticeps	0	0	0	0	7	63	19	7	0	0	4	27	LC
Kurtops signatus	0	0	0	0	11	53	21	11	3	0	3	38	LC
Milichus apicalis	0	0	0	0	50	0	0	50	0	0	0	4	LC (LLR)

Tribes and species (clades, see Figure 5)	% of Arid Namibia & Botswana ecoregions (AT 13++)						% of Mesic Namibia & Botswana savanna ecoregions (AT07++)					Total N 1/16th degree squares	Conservation status (low frequency)
	Succulent Karoo	Nama Karoo	Namib Desert	Kaokoveld Desert	Namibian Savanna Woodlands	Kalahari Xeric Savanna	Kalahari Acacia Baikiaea Woodlands	Zambezian & Mopane Woodlands	Angolan Mopane Woodlands	Southern African Bushveld	Zambezian Baikiaea Woodlands		
Mimonthophagus anomalus	0	0	0	0	0	0	0	100	0	0	0	3	LC (LLR)
Mimonthophagus limbibasis	0	0	0	0	0	0	100	0	0	0	0	1	DD (R, RR)
Onthophagus aequepubens	0	0	0	0	80	20	0	0	0	0	0	5	LC
Onthophagus aeruginosus	0	0	7	0	20	33	13	27	0	0	0	15	LC
Onthophagus albipodex	0	0	0	0	0	0	100	0	0	0	0	1	LC
Onthophagus apiciosus	0	0	0	0	0	0	0	100	0	0	0	1	LC
Onthophagus axillaris	0	0	14	0	43	43	0	0	0	0	0	14	DD
Onthophagus bayeri	0	0	0	0	50	50	0	0	0	0	0	8	DD
Onthophagus bicavifrons	0	0	0	0	47	29	18	6	0	0	0	17	LC
Onthophagus bovinus	0	0	0	0	30	30	10	0	30	0	0	10	LC
Onthophagus convexus	0	0	6	0	13	44	13	19	0	0	6	16	LC
Onthophagus ebenicolor	0	0	0	0	13	0	13	25	13	38	0	8	LC
Onthophagus ebenus	0	0	0	0	0	0	0	100	0	0	0	2	LC
Onthophagus fimetarius	0	0	0	0	58	11	0	11	16	0	5	19	LC
Onthophagus flavolimbatus	0	0	0	0	0	0	67	33	0	0	0	3	LC
Onthophagus gonopygus	0	0	27	13	60	0	0	0	0	0	0	15	LC
Onthophagus granulifer	0	0	0	0	4	61	22	4	4	0	4	23	LC
Onthophagus graphicus	0	0	0	0	100	0	0	0	0	0	0	1	DD
Onthophagus juvencus	0	0	0	0	0	0	0	0	0	0	100	1	LC
Onthophagus kochi	0	0	0	0	60	0	40	0	0	0	0	5	DD
Onthophagus lamelliger	0	0	0	0	0	0	22	33	0	33	11	9	LC
Onthophagus leucopygus	0	0	0	0	0	75	25	0	0	0	0	4	LC
Onthophagus obtusicornis	0	0	0	0	20	80	0	0	0	0	0	15	LC
Onthophagus pallidipennis	0	0	0	0	0	71	18	6	0	0	6	17	LC
Onthophagus plebejus	0	0	0	0	0	0	0	57	43	0	0	7	LC (LLR)
Onthophagus probus	0	4	31	0	50	15	0	0	0	0	0	26	LC
Onthophagus pullus	0	0	0	0	80	20	0	0	0	0	0	5	LC
Onthophagus quadrimaculatus	0	0	0	0	38	0	13	0	25	25	0	8	DD
Onthophagus quadrinodosus	0	0	0	0	0	60	0	20	0	0	20	5	LC
Onthophagus rasipennis	0	0	0	0	20	20	40	0	20	0	0	5	LC
Onthophagus semiflavus	0	3	26	3	42	23	3	0	0	0	0	31	LC

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APPENDIX 2: Summary Table 2. Distributions of 217 scarabaeine dung beetle species across ecoregions of Namibia and Botswana (Olson et al. 2001) represented by proportions of occupied 1/16th degree squares; data comprising 20% or greater of total records are highlighted in yellow; conservation status assessed using IUCN Red List categories (IUCN 2001) and frequency of records; see Synthesis section for key to division of tribes into clades of related species (continued)

Tribes and species (clades, see Figure 5)	% of Arid Namibia & Botswana ecoregions (AT 13++)						% of Mesic Namibia & Botswana savanna ecoregions (AT07++)					Total N 1/16th degree squares	Conservation status (low frequency)
	Succulent Karoo	Nama Karoo	Namib Desert	Kaokoveld Desert	Namibian Savanna Woodlands	Kalahari Xeric Savanna	Kalahari Acacia Baikiaea Woodlands	Zambezian & Mopane Woodlands	Angolan Mopane Woodlands	Southern African Bushveld	Zambezian Baikiaea Woodlands		
Onthophagini (Clade 23) (continued)													
Onthophagus suffusus	0	0	0	0	0	0	29	29	29	0	14	7	LC
Onthophagus tricorniger	0	0	0	0	40	20	0	0	40	0	0	5	DD
Onthophagus venustulus	0	0	2	0	28	34	19	6	6	0	4	47	LC
Onthophagus verticalis	0	0	0	0	0	56	17	11	6	0	11	18	LC
Onthophagus vinctus	0	0	0	0	31	16	20	18	4	2	8	49	LC
Onthophagus virescens	0	0	0	0	0	0	0	75	0	0	25	4	LC
Onthophagus vylderi	0	0	0	0	0	33	0	33	0	0	33	3	LC
Phalops ardea	0	0	0	0	0	0	0	0	50	50	0	2	LC
Phalops boschas	0	0	0	0	0	0	40	50	0	0	10	10	LC
Phalops dregei	0	0	0	0	0	0	33	17	33	17	0	6	LC
Phalops flavocinctus	0	0	0	0	0	0	40	40	0	20	0	5	LC
Phalops pauliani	0	0	0	0	9	64	0	0	27	0	0	11	LC
Phalops plancus	0	0	14	7	79	0	0	0	0	0	0	14	LC
Phalops prasinus	0	0	4	0	63	26	0	0	7	0	0	27	LC
Phalops pryroides	0	7	0	0	40	40	0	0	13	0	0	15	LC
Phalops rufosignatus	0	4	4	0	15	56	0	0	22	0	0	27	LC
Phalops smaragdinus	0	0	0	0	0	0	100	0	0	0	0	1	LC
Phalops wittei	0	2	4	0	15	50	13	2	12	0	2	52	LC
Phalops zuninoi	0	0	0	0	0	0	0	0	100	0	0	1	LC
Proagoderus bicallosus	0	0	0	0	0	0	0	50	13	0	38	8	LC (LLR)
Proagoderus furcifer	0	0	0	0	0	0	100	0	0	0	0	2	DD (R, LLR)
Proagoderus lanista	0	0	0	0	0	33	0	0	67	0	0	3	LC
Proagoderus loricatus	0	0	0	0	0	0	0	100	0	0	0	2	LC (LLR)
Proagoderus plato	0	0	0	0	0	0	0	0	0	0	100	1	DD (R, LLR)
Proagoderus rangifer	0	0	0	0	0	0	0	0	0	100	0	1	LC (LLR)
Proagoderus sapphirinus	0	0	0	0	17	63	8	8	4	0	0	24	LC
Scarabaeini (Clade 4)													
Escarabaeus remii	0	0	0	0	0	0	17	33	0	0	50	6	LC
Escarabaeus satyrus	3	10	12	5	39	23	5	1	0	1	0	77	LC

Tribes and species (clades, see Figure 5)	% of Arid Namibia & Botswana ecoregions (AT 13++)						% of Mesic Namibia & Botswana savanna ecoregions (AT07++)					Total N 1/16th degree squares	Conservation status (low frequency)
	Succulent Karoo	Nama Karoo	Namib Desert	Kaokoveld Desert	Namibian Savanna Woodlands	Kalahari Xeric Savanna	Kalahari Acacia Baikiaea Woodlands	Zambezian & Mopane Woodlands	Angolan Mopane Woodlands	Southern African Bushveld	Zambezian Baikiaea Woodlands		
Kheper cupreus	0	0	0	0	27	36	14	5	14	5	0	22	LC
Kheper kalaharicus	0	0	0	0	0	100	0	0	0	0	0	1	LC (RR)
Kheper lamarcki	0	0	0	0	0	46	12	38	0	4	0	26	LC
Kheper nigroaeneus	0	0	0	0	0	20	40	20	0	20	0	5	LC
Kheper prodigiosus	0	0	0	0	3	38	21	29	6	3	0	34	LC
Kheper subaeneus	0	0	0	0	0	0	67	0	0	33	0	3	LC
Kheper vethi	0	0	0	50	50	0	0	0	0	0	0	2	DD
Pachylomera femoralis	0	0	0	0	0	52	19	21	7	0	0	42	LC
Pachylomera opacus	0	0	0	0	0	80	20	0	0	0	0	5	LC
Pachysoma bennigseni	92	0	8	0	0	0	0	0	0	0	0	13	LC (RR)
Pachysoma denticolle	5	0	83	0	13	0	0	0	0	0	0	40	LC
Pachysoma fitzsimonsi	0	0	78	0	22	0	0	0	0	0	0	9	LC (RR)
Pachysoma gariepinum	85	15	0	0	0	0	0	0	0	0	0	20	LC
Pachysoma rodriguesi	0	0	96	0	4	0	0	0	0	0	0	23	LC
Pachysoma rotundigena	0	0	71	0	29	0	0	0	0	0	0	14	LC (RR)
Pachysoma schinzi	0	40	60	0	0	0	0	0	0	0	0	5	DD (RR)
Pachysoma valeflorae	100	0	0	0	0	0	0	0	0	0	0	2	DD (R, RR)
Scarabaeolus afronitidus	0	0	0	0	0	100	0	0	0	0	0	3	DD
Scarabaeolus anderseni	0	0	0	0	0	79	21	0	0	0	0	14	LC
Scarabaeolus bohemani	0	4	4	0	46	29	11	0	4	4	0	28	LC
Scarabaeolus canaliculatus	50	0	50	0	0	0	0	0	0	0	0	2	LC (R, RR)
Scarabaeolus carniphilus	0	0	0	0	0	100	0	0	0	0	0	2	DD
Scarabaeolus damarensis	0	0	0	0	0	60	10	25	5	0	0	20	LC
Scarabaeolus flavicornis	0	0	8	0	21	53	11	5	3	0	0	38	LC
Scarabaeolus fritschi	0	0	100	0	0	0	0	0	0	0	0	2	LC
Scarabaeolus inoportunus	0	0	0	0	0	78	22	0	0	0	0	9	LC
Scarabaeolus inquisitus	0	0	0	0	0	0	100	0	0	0	0	3	LC
Scarabaeolus karrooensis	0	0	25	0	50	25	0	0	0	0	0	4	LC
Scarabaeolus kochi	0	0	0	0	0	78	22	0	0	0	0	9	LC
Scarabaeolus lucidulus	0	0	0	0	0	0	75	0	0	0	25	4	DD
Scarabaeolus megaparvulus	0	13	25	0	50	13	0	0	0	0	0	8	LC
Scarabaeolus namibensis	0	0	78	0	22	0	0	0	0	0	0	9	LC

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Tribes and species (clades, see Figure 5)	% of Arid Namibia & Botswana ecoregions (AT 13++)						% of Mesic Namibia & Botswana savanna ecoregions (AT07++)					Total N 1/16th degree squares	Conservation status (low frequency)
	Succulent Karoo	Nama Karoo	Namib Desert	Kaokoveld Desert	Namibian Savanna Woodlands	Kalahari Xeric Savanna	Kalahari Acacia Baikiaea Woodlands	Zambezian & Mopane Woodlands	Angolan Mopane Woodlands	Southern African Bushveld	Zambezian Baikiaea Woodlands		
Scarabaeini (Clade 4) (continued)													
Scarabaeolus obsoletepunctatus	0	0	0	0	100	0	0	0	0	0	0	1	DD (R, RR)
Scarabaeolus pabulator	0	0	60	0	40	0	0	0	0	0	0	5	LC
Scarabaeolus parvulus	0	10	20	5	50	15	0	0	0	0	0	20	LC
Scarabaeolus rubripennis	17	0	71	0	13	0	0	0	0	0	0	24	LC
Scarabaeus alienus	0	0	100	0	0	0	0	0	0	0	0	1	DD (R)
Scarabaeus ambiguus	0	0	5	0	5	63	11	0	16	0	0	19	LC
Scarabaeus cognatus	0	0	40	20	40	0	0	0	0	0	0	5	DD
Scarabaeus costatus	0	27	27	9	18	18	0	0	0	0	0	11	LC
Scarabaeus deludens	0	0	0	0	25	0	25	0	50	0	0	4	LC
Scarabaeus funebris	0	0	0	0	0	0	0	0	100	0	0	3	DD (U)
Scarabaeus galenus	0	0	0	0	0	0	0	50	50	0	0	2	LC
Scarabaeus goryi	0	0	0	0	9	31	31	25	3	0	0	32	LC
Scarabaeus plausibilis	-	-	-	-	-	-	-	-	-	-	-	0	DD
Scarabaeus proboscideus	0	0	5	3	18	65	8	0	0	3	0	40	LC
Scarabaeus proximus	83	0	17	0	0	0	0	0	0	0	0	6	LC
Scarabaeus vicinus	0	0	0	0	0	78	11	0	11	0	0	9	LC
Scarabaeus zambesianus	0	0	0	0	0	22	44	30	0	0	4	27	LC
Sceliages granulatus	0	0	0	0	0	100	0	0	0	0	0	2	LC
Sisyphini (Clade 18)													
Neosisyphus calcaratus	0	0	0	0	0	29	14	43	0	14	0	7	LC
Neosisyphus macrorubrus	0	0	0	0	0	0	0	0	100	0	0	3	LC
Neosisyphus rubrus	0	0	0	0	0	50	0	0	0	50	0	2	LC
Sisyphus alveatus	0	0	0	0	0	0	0	0	0	0	100	1	LC
Sisyphus goryi	0	0	0	0	22	0	22	33	0	22	0	18	LC
Sisyphus impressipennis	0	0	0	0	100	0	0	0	0	0	0	1	LC
Sisyphus splendidus	0	0	0	0	50	50	0	0	0	0	0	2	DD
Total number of species	12	27	53	15	111	129	120	99	83	42	60	216	

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APPENDIX 3: Summary of average climatic, topographical and distributional data for dung beetle species recorded in South Africa, Botswana and Namibia

Species/subspecies (Generalised distribution patterns) (See summaries in Table 2)	Average data* (see species accounts for SD)			Endemic status**	Main distribution patterns in RSA, Botswana, Namibia (see Fig. 6, Summary Tables 2, 3, & species accounts)	N 5×5 km² polygons*	EOO (km²)
	Annual temperature (°C)	Annual rainfall (mm)	Altitude (m)				
Tribe ATEUCHINI (Figs 6A, 6D)							
Coptorhina auspicata (NE6)	19.55	610	1 139		E Savanna / Kalahari	56	898 960
Coptorhina excavata (E4)	16.43	586	1 451	Endemic	Highveld (Grassland)	8	115 840
Coptorhina klugii (NE6)	19.53	751	646		E Savanna / Highveld (N Grassland)	73	681 450
Coptorhina nitidipennis (NE6)	20.25	722	837		E Savanna	39	4 106 325
Delopleurus darrenmanni (NE2)	22.30	609	907		W Savanna - N Botswana	3	22 265
Delopleurus gilleti (NE2)	21.02	678	791		W Savanna - N Namibia	4	1 773 210
Delopleurus pullus (NE7)	19.66	701	1 063		Savanna (E & W)	23	186 855
Frankenbergerius armatus armatus (E7)	17.99	778	376	Endemic	E Coast (Forest)	14	43 660
Frankenbergerius armatus tuberculatus (E4)	17.25	839	1 216	Endemic	Highveld (E Forest)	17	21 915
Frankenbergerius barratti (E4)	16.33	768	1 320	Endemic	Highveld (Grassland)	8	16 485
Frankenbergerius forcipatus (E4)	15.22	662	1 220	Endemic	Highveld (SE?Forest)	6	21 625
Frankenbergerius gomesi (E4)	18.54	805	943	Endemic	Highveld (NE Forest) / E Savanna	13	18 695
Frankenbergerius nanus (E1)	15.05	436	339	Endemic	SW Cape (Fynbos)	4	2 995
Frankenbergerius nitidus (E1)	18.15	140	1	Endemic	SW Cape - Namaqualand (Succulent Karoo)	1	?
Frankenbergerius opacus (E1)	16.90	435	228	Endemic	SW Cape (Fynbos)	1	?
Pedaria barrei (NE6)	21.83	560	496		E Savanna	7	1 460 055
Pedaria brancoi (NE7)	20.86	729	1 087		Savanna (E & W)	8	809 330
Pedaria cylindrica (NE6)	20.26	612	810		E Savanna	22	127 365
Pedaria picea (E10)	19.29	664	860	Endemic	E Savanna	73	388 675
Pedaria segregis (NE6)	21.99	704	213		E Savanna	33	730 030
Sarophorus angolensis (NE2)	18.15	583	1 372		W Savanna - Arid NW Namibia	2	3 760
Sarophorus bidentatus (E1)	15.50	162	1 070	Endemic	SW Cape - Namaqualand (Succulent Karoo)	1	?
Sarophorus carinatus (E4)	16.78	875	1 281	Endemic	Highveld (E Woodland)	2	755
Sarophorus costatus (NE6)	19.26	674	926		E Savanna / Highveld (N Grassland)	139	283 960
Sarophorus diabolus (E1)	16.90	350	334	Endemic	SW Cape (Fynbos)	2	?
Sarophorus frolovi (E4)	15.30	815	1 187	Endemic	Highveld (SE Forest)	1	?
Sarophorus latus (E10)	19.03	633	1 091	Endemic	E Savanna	4	12 270
Sarophorus punctatus (E2)	17.95	458	0	Endemic	S Cape (Forest)	1	?
Sarophorus striatus (E2)	17.18	501	371	Endemic	S Cape (Albany Thicket, Fynbos)	13	6740
Sarophorus tuberculatus (E2)	15.92	386	445	Endemic	SW Cape / S Cape (Fynbos, Albany Thicket)	17	46 695

*Average data for total 5×5 km2 polygons occupied in Africa south of 15°S.
**Endemic to South Africa, Botswana and/or Namibia; absence of an entry = non-endemic species.
***Does not include type locality.

APPENDIX 3: Summary of average climatic, topographical and distributional data for dung beetle species recorded in South Africa, Botswana and Namibia (continued)

Species/subspecies (Generalised distribution patterns) (See summaries in Table 2)	Average data* (see species accounts for SD)			Endemic status**	Main distribution patterns in RSA, Botswana, Namibia (see Fig. 6, Summary Tables 2, 3, & species accounts)	N 5×5 km² polygons*	EOO (km²)
	Annual temperature (°C)	Annual rainfall (mm)	Altitude (m)				
Tribe CANTHONINI (Figs 6B, 6C, 6F, 6G)							
Aliuscanthoniola similaris (E7)	19.70	961	58	Endemic	E Coast (Forest)	1	?
Aphengoecus clypeatus (E1)	16.90	435	228	Endemic	SW Cape (Fynbos)	1	?
Aphengoecus multiserratus (E1)	17.08	245	194	Endemic	SW Cape - West Coast (Fynbos)	16	3 700
Bohepilissus nitidus (E1)	14.07	487	485	Endemic	SW Cape (Forest)	6	25
Bohepilissus subtilis (E2)	16.21	492	422	Endemic	S Cape (Forest)	29	38 100
Byrrhidium convexum (E1)	16.61	57	452	Endemic	SW Cape - Richtersveld (Succulent Karoo)	7	163
Byrrhidium ovale (E1)	16.77	143	689	Endemic	SW Cape - Namaqualand (Succulent Karoo)	6	2 370
Chalconotus convexus (NE7)	20.30	646	790		Savanna (E & W)	335	6 750 790
Circellium bacchus (E2)	17.24	431	151	Endemic	S Cape (Fynbos, Albany Thicket)	24	11 950
Dicranocara deschodti (E5)	16.54	81	769	Endemic	SW Arid - S Namibia (Nama Karoo)	5	190
Dicranocara inexpectata (E5)	16.90	99	867	Endemic	SW Arid - S Namibia (Nama Karoo)	1	?
Dicranocara tatasensis (E1)	17.70	53	372	Endemic	SW Cape - Richtersveld (Succulent Karoo)	1	3.3
Dicranocara vandersmisseni (E5)	19.55	91	449	Endemic	SW Arid - S Namibia (Nama Karoo)	2	300
Drogo stalsi (E5)	12.85	123	1 608	Endemic	SW Arid - S Namibia (Nama Karoo)	1	?
Dwesasilvisedis medinae (E7)	18.90	899	112	Endemic	E Coast (Forest)	1	28.6
Endroedyolus paradoxus (E4)	15.55	1 111	1 170	Endemic	Highveld (SE Forest)	2	80
Epirinus aeneus (E1)	17.55	231	652	Endemic	SW Cape (Fynbos) / Nama Karoo	125	335 500
Epirinus aquilus (E2)	16.75	539	402	Endemic	S Cape (Forest)	2	130
Epirinus asper (E4)	13.74	854	1 763	Endemic	Highveld (NE Grassland)	18	40 500
Epirinus bentoi (E1)	17.33	226	91	Endemic	SW Cape - West Coast (Fynbos, Succ. Karoo)	12	2 700
Epirinus comosus (E1)	16.01	375	381	Endemic	SW Cape / S Cape (Fynbos)	14	27 500
Epirinus convexus (E7)	18.78	869	225	Endemic	E Coast (Forest)	6	2 300
Epirinus davisi (E7)	20.55	988	258	Endemic	NE Coast - KZN (Forest)	2	81
Epirinus drakomontanus (E4)	7.78	877	2 731	Endemic	Highveld (E Grassland)	3	80
Epirinus flagellatus (E1)	16.08	302	540	Endemic	SW Cape / S Cape (Fynbos, Succulent Karoo)	110	258 000
Epirinus granulatus (E1)	17.25	216	130	Endemic	SW Cape - West Coast (Fynbos, Succ. Karoo)	11	3 400
Epirinus gratus (E4)	17.22	542	1 379	Endemic	Highveld (NW Grassland)	23	74 300
Epirinus hilaris (E2)	15.28	451	609	Endemic	S Cape (Fynbos)	17	29 550
Epirinus hluhluwensis (E7)	20.45	900	273	Endemic	NE Coast - KZN (Forest)	1	1 580
Epirinus minimus (E2)	17.35	462	61	Endemic	S Cape (Forest)	2	1 130
Epirinus montanus (E2)	12.45	331	1 442	Endemic	S Cape (Fynbos)	2	1 750
Epirinus mucrodentatus (E4)	15.28	885	1 534	Endemic	Highveld (NE)	3	170

Species/subspecies (Generalised distribution patterns) (See summaries in Table 2)	Average data* (see species accounts for SD)			Endemic status**	Main distribution patterns in RSA, Botswana, Namibia (see Fig. 6, Summary Tables 2, 3, & species accounts)	N 5×5 km² polygons*	EOO (km²)
	Annual temperature (°C)	Annual rainfall (mm)	Altitude (m)				
Epirinus ngomae (E4)	17.55	858	999	Endemic	Highveld (E Forest)	1	765
Epirinus obtusus (E4)	15.60	494	1 039	Endemic	Highveld (SE Grassland) / Albany Thicket	26	106 900
Epirinus pseudorugosus (E1)	15.80	302	63	Endemic	SW Cape - West Coast (Fynbos)	7	230
Epirinus punctatus (E4)	13.20	954	1 820	Endemic	Highveld (E Forest)	5	17 500
Epirinus pygidialus (E4)	11.50	815	2 100	Endemic	Highveld (E?Forest)	4	7 810
Epirinus relictus (E4)	11.84	701	1 761	Endemic	Highveld (E Grassland) / S Cape (Fynbos)	11	50 250
Epirinus rugosus (E1)	13.20	273	1 453	Endemic	SW Cape (Fynbos)	3	15
Epirinus scrobiculatus (E1)	17.33	197	177	Endemic	SW Cape - West Coast (Fynbos, Succ. Karoo)	25	15 275
Epirinus sebastiani (E4)	14.28	705	1 242	Endemic	Highveld (SE Forest)	2	130
Epirinus silvestris (E2)	16.87	481	237	Endemic	S Cape (Forest)	14	1 175
Epirinus striatus (E3)	15.22	306	1 352	Endemic	Upper Karoo	53	98 000
Epirinus sulcipennis (E2)	10.90	379	1 546	Endemic	S Cape (Fynbos)	1	?
Epirinus validus (E4)	12.95	793	1 772	Endemic	Highveld (E Grassland)	26	52 550
Gyronotus carinatus (E7)	21.05	964	115	Endemic	NE Coast - KZN (Forest)	5	2 900
Gyronotus glabrosus (E4)	16.20	869	1 363	Endemic	Highveld (NE Grassland)	6	1 270
Gyronotus perissinottoi (E7)	19.35	966	161	Endemic	E Coast (Grassland)	1	?
Gyronotus pumilus (E7)	19.51	914	119	Endemic	E Coast (Forest)	18	6 350
Gyronotus schuelei (E4)	19.10	922	870	Endemic	Highveld (NE Grassland)	2	83
Hammondantus psammophilus (E5)	16.11	76	845	Endemic	SW Arid - Namib Desert	6	13 600
Namakwanus irishi (E5)	18.30	353	1 815	Endemic	SW Arid - Arid Namibian Savanna	1	?
Namakwanus scholtzi (E5)	16.65	18	400	Endemic	SW Arid - Namib Desert	1	?
Namaphilus ameibensis (E5)	17.50	210	1 197	Endemic	SW Arid - Arid Namibian Savanna	1	?
Namaphilus davisi (E5)	21.00	176	1 164	Endemic	SW Arid - Arid Namibian Savanna	1	25
Namaphilus endroedyi (E5)	15.72	155	1 474	Endemic	SW Arid - Arid Namibian Savanna	3	280
Nebulasilvius insularis (E4)	16.85	847	974	Endemic	Highveld (SE Forest)	1	?
Nebulasilvius johani (E4)	15.35	815	1 179	Endemic	Highveld (SE Forest)	2	1.7
Odontoloma apiculum (E2)	18.28	411	227	Endemic	S Cape (Forest)	2	905
Odontoloma dentinum (E1)	16.95	316	179	Endemic	SW Cape / S Cape (Fynbos, Succulent Karoo)	21	52 460
Odontoloma disalatum (E1)	16.89	266	289	Endemic	SW Cape (Fynbos)	11	43 165
Odontoloma doubei (E4)	14.80	833	1 206	Endemic	Highveld (E Grassland)	6	13 375
Odontoloma endroedyi (E2)	15.04	313	913	Endemic	S Cape (Fynbos, Succulent Karoo)	11	45 810
Odontoloma louwi (E4)	18.57	339	1 305	Endemic	Highveld (Grassland) / W Savanna - N Namibia	11	131 940

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***Does not include type locality.

APPENDIX 3: Summary of average climatic, topographical and distributional data for dung beetle species recorded in South Africa, Botswana and Namibia (continued)

Species/subspecies (Generalised distribution patterns) (See summaries in Table 2)	Average data* (see species accounts for SD)			Endemic status**	Main distribution patterns in RSA, Botswana, Namibia (see Fig. 6, Summary Tables 2, 3, & species accounts)	N 5×5 km² polygons*	EOO (km²)
	Annual temperature (°C)	Annual rainfall (mm)	Altitude (m)				
Tribe CANTHONINI (Figs 6B, 6C, 6F, 6G) (continued)							
Odontoloma obscurum (E4)	11.39	688	1 838	Endemic	Highveld (SE Grassland)	5	8 020
Odontoloma pauxillum (NE6)	20.13	629	924		E Savanna	6	1 021 080
Odontoloma peckorum (E4)	14.40	816	1 544	Endemic	Highveld (E Grassland)	12	19 885
Odontoloma planatum (E4)	16.31	900	1 096	Endemic	Highveld (E Grassland)	7	14 615
Odontoloma pusillum (E1)	16.60	273	94	Endemic	SW Cape - West Coast (Fynbos)	5	1 685
Odontoloma pygidiale (E1)	16.81	243	334	Endemic	SW Cape (Fynbos, Succulent Karoo)	47	71 165
Odontoloma quadridens (NE6)	20.30	486	1 040		E Savanna	3	15 205
Odontoloma sculpturatum (E4)	16.29	597	861	Endemic	Highveld (E Grassland) / S Cape	7	64 415
Odontoloma spinicaudum (E1)	18.15	142	38	Endemic	SW Cape - Namaqualand (Succulent Karoo)	1	?
Outenikwanus tomentosus (E2)	13.75	404	999	Endemic	S Cape (Forest)	1	?
Parvuhowdenius harrisoni (E4)	14.65	855	1 364	Endemic	Highveld (SE Forest)	1	16.9
Peckolus alpinus (E4)	15.98	891	1 410	Endemic	Highveld (NE Forest)	2	15
Peckolus parvus (E4)	9.15	810	2 497	Endemic	Highveld (E Forest)	1	1.4
Peckolus poenskopius (E4)	17.98	1 005	1 085	Endemic	Highveld (NE Forest)	3	85
Pycnopanelus krikkeni (E9)	18.84	191	987	Endemic	SW Arid (Nama Karoo, Arid Namibian Savanna)	110	264 500
Silvaphilus oubosiensis (E1)	16.30	367	389	Endemic	SW Cape (Forest)	1	6
Versicorpus erongoensis (E5)	17.50	210	1 197	Endemic	SW Arid - Arid Namibian Savanna	1	?
Versicorpus streyi (E5)	15.85	179	1 621	Endemic	SW Arid - Arid Namibian Savanna	1	?
Tribe COPRINI (Figs 6D, 6E, 6G)							
Catharsius aegeus (NE6)	20.72	631	792		E Savanna	48	812 345
Catharsius calaharicus (E8)	19.86	329	1 062	Endemic	Kalahari	152	639 850
Catharsius harpagus (NE3)	22.23	801	28		NE Coast - KZN	12	8 250
Catharsius heros (NE7)	21.26	538	895		Savanna (E & W) / Kalahari	32	3 687 200
Catharsius laticeps (NE6)	22.83	513	308		E Savanna	4	15 750
Catharsius longiceps (E4)	16.82	657	1 470	Endemic	Highveld (Grassland)	10	6 130
Catharsius marcellus (E4)	15.16	802	1 533	Endemic	Highveld (Grassland)	37	126 300
Catharsius melancholicus (NE4)	19.98	338	1 050		Kalahari	45	970 820
Catharsius pandion (NE3)	21.91	853	43		NE Coast - KZN	52	18 650
Catharsius philus (NE6)	20.51	627	783		E Savanna	94	774 500
Catharsius platycerus (NE6)	23.16	704	568		E Savanna	8	3 012 810
Catharsius sesostris (NE6)	19.31	757	993		E Savanna / Highveld (Grassland)	96	5 293 770
Catharsius tricornutus (NE7)	18.92	701	873		Savanna (E & W), Highveld (Grassland), S Cape	205	1 064 120

Species/subspecies (Generalised distribution patterns) (See summaries in Table 2)	Average data* (see species accounts for SD)			Endemic status**	Main distribution patterns in RSA, Botswana, Namibia (see Fig. 6, Summary Tables 2, 3, & species accounts)	N 5×5 km² polygons*	EOO (km²)
	Annual temperature (°C)	Annual rainfall (mm)	Altitude (m)				
Catharsius ulysses (E4)	18.87	454	1 307	Endemic	Highveld (Grassland) / W Savanna - N Namibia	70	367 200
Catharsius vitulus (E4)	15.30	404	1 385	Endemic	Highveld (Grassland) / Upper Karoo	40	92 235
Copris amyntor (NE6)	20.73	631	739		E Savanna	255	1 016 860
Copris anceus (E1)	16.70	270	77	Endemic	SW Cape - W Coast (Fynbos)	35	7 625
Copris antares (E4)	16.47	628	1 136	Endemic	Highveld (Grassland)	61	269 985
Copris bootes (NE6)	22.39	740	497		E Savanna	19	959 800
Copris caelatus (E4)	14.85	792	1 480	Endemic	Highveld (E Grassland))	40	91 950
Copris cambeforti (E10)	20.00	578	952	Endemic	E Savanna	2	540
Copris capensis (E1)	17.14	205	175	Endemic	SW Cape (Fynbos, Succulent Karoo)	43	45 395
Copris cassius (E8)	19.22	372	1 161	?Endemic	Kalahari (SW)	92	547 290
Copris cornifrons (E8)	19.37	312	1 111	Endemic	Kalahari (SW)	38	286 300
Copris corniger (E4)	15.50	718	1 356	Endemic	Highveld (Grassland)	90	318 935
Copris crassus (E4)	14.98	721	1 437	Endemic	Highveld (E Grassland))	8	41 240
Copris denticulatus (NE6)	19.64	690	927		E Savanna	182	940 275
Copris elphenor (NE7)	20.02	581	972		Savanna (E & W)	420	3 968 365
Copris evanidus (NE6)	20.56	564	802		E Savanna	217	2 357 905
Copris fidius (NE1)	17.63	755	650		Highveld (E Forest) / E Coast / S Cape (Forest)	110	116 200
Copris gracilis (E6)	19.29	340	1 394	Endemic	W Savanna - N Namibia	54	168 350
Copris inhalatus perturbator (NE4)	19.91	492	1 147		Kalahari	14	614 150
Copris inhalatus sanctaeluciae (NE3)	22.02	831	34		NE Coast - KZN	27	8 520
Copris jacchoides (E4)	15.27	724	1 430	Endemic	Highveld (Grassland)	52	258 970
Copris jacchus (E2)	17.51	462	244	Endemic	S Cape (Albany Thicket, Fynbos)	6	9 990
Copris laioides (E6)	20.59	446	1 429	Endemic	W Savanna - N Namibia	20	49 485
Copris macer (NE6)	17.89	846	1 153		E Savanna / Highveld (Grassland)	39	65 380
Copris mesacanthus mesacanthus (NE6)	20.90	791	894		E Savanna	20	378 400
Copris mesacanthus transvaalensis (NE6)	19.43	670	944		E Savanna	133	223 300
Copris obesus (NE1)	17.68	752	1 237		Highveld (NE Grassland)	171	1 252 590
Copris orion caffer (E7)	19.38	806	189	Endemic	E Coast / Albany Thicket	23	31 800
Copris puncticollis (NE7)	22.26	778	245		Savanna (E & W) / NE Coast - KZN	43	211 185
Copris ritsemae (E4)	17.27	724	1 356	Endemic	Highveld (N Grassland)	10	18 840
Copris sexdentatus (E2)	17.62	427	88	Endemic	S Cape (Fynbos)	3	3 945
Copris sphaeropterus (E2)	16.40	422	152	Endemic	S Cape (Fynbos)	1	?

*Average data for total 5×5 km2 polygons occupied in Africa south of 15°S.
**Endemic to South Africa, Botswana and/or Namibia; absence of an entry = non-endemic species.
***Does not include type locality.

APPENDIX 3: Summary of average climatic, topographical and distributional data for dung beetle species recorded in South Africa, Botswana and Namibia (continued)

Species/subspecies (Generalised distribution patterns) (See summaries in Table 2)	Average data* (see species accounts for SD)			Endemic status**	Main distribution patterns in RSA, Botswana, Namibia (see Fig. 6, Summary Tables 2, 3, & species accounts)	N 5×5 km² polygons*	EOO (km²)
	Annual temperature (°C)	Annual rainfall (mm)	Altitude (m)				
Tribe COPRINI (Figs 6D, 6E, 6G)							
Copris subsidens (E6)	19.05	340	1 366	Endemic	W Savanna - N Namibia	58	105 070
Copris urus (NE3)	21.91	847	42		NE Coast KZN	25	8 690
Copris victorini (E2)	16.06	425	437	Endemic	S Cape (Fynbos)	4	2 100
Copris vilhenai (NE6)	20.81	630	867		E Savanna	43	677 310
Copris vrydaghi (E4)	16.90	758	1 070	Endemic	Highveld (E Grassland)	4	5 085
Heliocopris andersoni (NE7)	19.61	567	1 057		Savanna (E & W)	103	3 715 845
Heliocopris atropos (NE4)	20.01	493	1 113		Kalahari / East Savanna	44	1 602 870
Heliocopris faunus (NE7)	18.36	376	1 177		Savanna (E & W) / Upper Karoo	69	391 450
Heliocopris hamadryas (NE6)	18.60	678	1 068		E Savanna / Highveld (Grassland)	155	3 416 220
Heliocopris japetus (NE4)	20.46	569	1 020		Kalahari / E Savanna	137	3 260 895
Heliocopris neptunus (NE6)	19.92	653	824		E Savanna	83	328 720
Heliocopris pirmal (NE6)	18.70	702	1 085		E Savanna / Highveld (NE Grassland)	64	236 025
Litocopris muticus (NE6)	22.17	912	257		E Savanna	11	793 435
Litocopris simplex (E7)	16.74	684	695	Endemic	E Coast / Highveld (E Grassland)	45	85 760
Macroderes amplior (E1)	17.58	134	388	Endemic	SW Cape - Namaqualand (Succulent Karoo)	3	1 170
Macroderes arrowi (E1)	18.73	161	218	Endemic	SW Cape - Namaqualand (Succulent Karoo)	2	52.5
Macroderes bias (E2)	15.54	432	839	Endemic	S Cape (Albany Thicket, Fynbos)	9	40 815
Macroderes cornutus (E1)	17.41	115	73	Endemic	SW Cape - Namaqualand (Succulent Karoo)	4	2 605
Macroderes endroedyi (E1)	17.69	204	162	Endemic	SW Cape - W Coast (Fynbos, Succulent Karoo)	9	2 775
Macroderes fornicatus (E1)	15.23	454	235	Endemic	SW Cape (Fynbos)	2	535
Macroderes foveatus (E1)	16.55	255	20	Endemic	SW Cape - West Coast (Fynbos, Succ. Karoo)	2	105
Macroderes greeni (E1)	16.07	324	47	Endemic	SW Cape (Fynbos)	7	1 535
Macroderes minutus (E1)	18.42	155	257	Endemic	SW Cape - Namaqualand (Succ. Karoo, Fynbos)	6	5 045
Macroderes mutilans (E1)	16.96	129	871	Endemic	SW Cape - Namaqualand (Succulent Karoo)	5	1 501
Macroderes namakwanus (E1)	17.94	126	148	Endemic	SW Cape - Namaqualand (Succulent Karoo)	5	53
Macroderes nitidus (E1)	17.03	169	791	Endemic	SW Cape - Namaqualand (Succulent Karoo)	2	80
Macroderes politulus (E1)	16.47	356	320	Endemic	SW Cape (Fynbos)	8	7 940
Macroderes undulatus (E1)	16.65	388	277	Endemic	SW Cape (Fynbos)	4	2 300
Metacatharsius anderseni (E8)	19.57	266	1 077	Endemic	Kalahari (SW)	52	255 955
Metacatharsius dentinum (NE4)	19.51	294	1 034		Kalahari / Nama Karoo	114	1 080 805
Metacatharsius exiguiformis (E8)	19.30	248	1 041	Endemic	Kalahari (SW) / Nama Karoo / Arid W Savanna	168	471 130
Metacatharsius exiguus (NE4)	20.67	557	827		Kalahari / East Savanna / NE Coast - KZN	40	680 625

Species/subspecies (Generalised distribution patterns) (See summaries in Table 2)	Average data* (see species accounts for SD)			Endemic status**	Main distribution patterns in RSA, Botswana, Namibia (see Fig. 6, Summary Tables 2, 3, & species accounts)	N 5×5 km² polygons*	EOO (km²)
	Annual temperature (°C)	Annual rainfall (mm)	Altitude (m)				
Metacatharsius ferreirae (NE4)	21.95	459	951		Kalahari / East Savanna	8	923 845
Metacatharsius freyi (E8)	20.78	412	994	Endemic	Kalahari / East Savanna	10	257 510
Metacatharsius latifrons (E8)	18.45	279	975	Endemic	Kalahari (SW) / SW Cape - West Coast (SKaroo)	91	322 620
Metacatharsius marani (E9)	18.45	223	1 083	Endemic	SW Arid (Nama Karoo, Arid W Savanna)	239	312 390
Metacatharsius opacus (NE7)	21.33	560	771		Savanna (E & W)	189	3 129 685
M. pumilioniformis / pumilionis (E8)	19.69	398	1 000	Endemic	Kalahari / E Savanna	43	688 900
Metacatharsius troglodytes (NE7)	20.62	538	934		Savanna (E & W)	173	1 228 465
Metacatharsius zuluanus (NE3)	22.49	708	132		NE Coast - KZN / E Savanna	19	30 915
Xinidium dentilabris (E4)	15.47	838	1 394	Endemic	Highveld (E Grassland)	103	107 815
Xinidium dewitzi (E4)	15.05	813	1 287	Endemic	Highveld (E Forest)	4	5 990
Xinidium howdeni (E4)	10.90	768	1 707	Endemic	Highveld (E Forest)	3	20
Tribe GYMNOPLEURINI (Fig. 6H)							
Allogymnopleurus consocius (E7)	20.19	710	540	Endemic	NE Coast - KZN / Highveld (N Grassland)	11	35 250
Allogymnopleurus splendidus (NE7)	19.49	477	956		Savanna (E & W) / Upper Karoo	413	1 523 140
Garreta australugens (NE6)	22.64	659	405		E Savanna	7	88 890
Garreta caffer (NE3)	22.04	849	12		NE Coast - KZN	26	8 394
Garreta laetus olivaceus (NE6)	21.23	913	754		E Savanna (Forest)	18	2 848 875
Garreta nitens (NE2)	20.36	545	1 282		W Savanna - N Namibia	26	4 761 275
Garreta unicolor (NE6)	17.32	797	1 111		E Savanna / Highveld (N Grassland)	98	209 670
Garreta wahlbergi (NE6)	20.33	643	857		E Savanna	209	737 635
Gymnopleurus aenescens (NE7)	19.75	354	978		Savanna (E & W) / Kalahari / Upper Karoo	157	1 407 890
Gymnopleurus andreaei (NE5)	18.60	188	1 003		SW Arid (Nama Karoo, Arid W Savanna)	143	263 705
Gymnopleurus asperrimus (E9)	18.92	206	1 020	Endemic	SW Arid (Nama Karoo) / Kalahari (SW)	187	223 500
Gymnopleurus humanus (NE5)	17.93	231	1 106		SW Arid (Nama Karoo, Arid W Savanna)	380	587 750
Gymnopleurus humeralis (NE6)	20.94	601	735		E Savanna	115	534 260
Gymnopleurus ignitus (NE4)	22.80	652	706		Kalahari (NE)	24	659 605
Gymnopleurus leei (E4)	15.59	514	1 335	Endemic	Highveld (Grassland) / S Cape	74	256 000
Gymnopleurus pumilus (NE7)	20.77	550	850		Savanna (E & W)	141	451 400
Gymnopleurus reichei (NE6)	22.89	521	256		E Savanna	4	253 700
Gymnopleurus thelwalli (NE6)	21.52	661	617		E Savanna	7	555 105
Gymnopleurus virens (NE6)	18.53	739	1 089		E Savanna	114	267 770

*Average data for total 5×5 km2 polygons occupied in Africa south of 15°S.
**Endemic to South Africa, Botswana and/or Namibia; absence of an entry = non-endemic species.
***Does not include type locality.

APPENDIX 3: Summary of average climatic, topographical and distributional data for dung beetle species recorded in South Africa, Botswana and Namibia (continued)

Species/subspecies (Generalised distribution patterns) (See summaries in Table 2)	Average data* (see species accounts for SD)			Endemic status**	Main distribution patterns in RSA, Botswana, Namibia (see Fig. 6, Summary Tables 2, 3, & species accounts)	N 5×5 km² polygons*	EOO (km²)
	Annual temperature (°C)	Annual rainfall (mm)	Altitude (m)				
Tribe ONITICELLINI (Fig. 6I)							
Afrodrepanus impressicollis (E7)	19.50	875	595	Endemic	NE Coast - KZN / E Savanna (NE Forest)	32	27 860
Cyptochirus ambiguus (NE1)	16.94	775	1 046		Highveld (Grassland) / E Savanna	112	323 350
Drepanocerus kirbyi (NE6)	18.45	733	883		E Savanna / Highveld (Grassland)	112	3 526 325
Drepanocerus patrizii (NE6)	18.01	536	1 129		E Savanna / Highveld (Grassland)	41	503 040
Eodrepanus bechynei (NE3)	20.24	1 021	421		NE Coast - KZN / East Savanna	6	2 080 435
Eodrepanus fastiditus (NE6)	18.47	763	941		E Savanna / Highveld (Grassland)	56	1 517 320
Eodrepanus parallelus (NE3)	20.98	755	754		NE Coast - KZN / E Savanna	8	797 475
Epidrepanus caelatus (NE1)	17.23	786	1 199		Highveld (Grassland)	24	160 840
Euoniticellus africanus (E4)	15.75	518	1 218	Endemic	Highveld (Grassland)	215	677 390
Euoniticellus intermedius (NE7)	18.70	507	967		Savanna (E & W), SW Arid, SW Cape, S Cape	580	9 060 360
Euoniticellus kawanus (NE7)	20.64	444	968		Savanna (E & W)	8	2 691 645
Euoniticellus triangulatus (NE1)	16.91	673	887		Highveld (Grassland) / E Savanna / S Cape	178	2 234 985
Euoniticellus zumpti (NE3)	21.37	778	310		NE Coast - KZN / E Savanna	15	273 965
Ixodina abyssinica (NE3)	21.34	888	229		NE Coast - KZN	6	347 255
Latodrepanus laticollis (NE6)	20.40	701	832		E Savanna	80	4 469 700
Liatongus militaris (NE6)	18.42	720	949		E Savanna / Highveld (Grassland)	315	3 632 435
Oniticellus egregius (NE7)	20.67	597	748		Savanna (E & W)	38	2 407 180
Oniticellus formosus (NE6)	20.39	608	752		E Savanna	77	4 827 535
Oniticellus pictus (NE1)	16.49	661	834		Highveld (E Grassland) / S Cape	35	131 510
Oniticellus planatus (NE6)	18.84	731	791		E Savanna / Highveld (NE Grassland) / S Cape	186	4 837 160
Paraixodina freyi (NE3)	21.18	795	247		NE Coast - KZN / E Savanna	9	450 215
Paraixodina saegeri (NE6)	21.73	668	480		E Savanna	12	1 073 235
Tibiodrepanus sulcicollis (NE1)	16.55	725	893		Highveld (SE Grassland) / E Coast	38	5 683 200
Tiniocellus eurypygus eurypygus (E10)	18.7	638	1 212	Endemic	E Savanna	32	39 045
T. eurypygus transdrakensbergensis (E10)	21.13	700	467	Endemic	E Savanna	35	84 580
Tiniocellus spinipes (NE6)	22.60	636	470		E Savanna	27	2 951 525
Tragiscus dimidiatus (NE7)	22.39	602	471		Savanna (E & W)	24	2 192 230
Tribe ONITINI (Fig. 6J)							
Anonychonitis freyi (E7)	20.80	878	199	Endemic	NE Coast - KZN / E Savanna	5	960
Cheironitis audens (E9)	17.93	241	1 100	Endemic	SW Arid (Nama Karoo, Arid W Savanna)	105	208 930
Cheironitis hoplosternus (E4)	17.67	353	1 187	Endemic	Highveld (Grassland) / Upper Karoo / N Namibia	138	651 685
Cheironitis imitator (NE6)	22.29	486	541		E Savanna	16	669 950

Species/subspecies (Generalised distribution patterns) (See summaries in Table 2)	Average data* (see species accounts for SD)			Endemic status**	Main distribution patterns in RSA, Botswana, Namibia (see Fig. 6, Summary Tables 2, 3, & species accounts)	N 5×5 km² polygons*	EOO (km²)
	Annual temperature (°C)	Annual rainfall (mm)	Altitude (m)				
Cheironitis indicus (E9)	18.51	196	1 028	Endemic	SW Arid (Nama Karoo, Arid W Savanna)	61	113 785
Cheironitis scabrosus (E9)	17.59	244	1 017	Endemic	SW Arid (Nama Karooa) / SW Cape	242	478 375
Gilletellus porculus (E6)	22.2	391	1 156	Endemic	W Savanna - N Namibia	1	?
Heteronitis castelnaui (NE7)	22.03	605	565		Savanna (E & W)	74	3 997 830
Kolbeellus ateuchoides (E3)	11.85	429	1 890	Endemic	Upper Karoo	2	1 395
Megalonitis bohemani (NE7)	22.39	528	928		Savanna (E & W)	7	317 740
Neonitis nigritiae (NE6)	18.68	748	1 355		E Savanna	4	123 785
Onitis aeruginosus (NE6)	22.96	586	701		E Savanna	10	134 325
Onitis alexis (NE7)	19.27	600	981		Savanna (E & W) / Highveld (Grassland)	574	9 990 325
Onitis aygulus (E3)	16.88	356	971	Endemic	Upper Karoo / S Cape	157	756 700
Onitis bilobatus (E6)	17.00	367	1 264	Endemic	W Savanna - N Namibia	1	?
Onitis caffer (E4)	17.01	585	990	Endemic	Highveld (Grassland) / E Savanna / S Cape	275	576 190
Onitis confusus (E3)	16.55	298	603	Endemic	SW Cape / Upper Karoo	34	529 675
Onitis cribratus (E4) ***	14.63	762	1 430	Endemic	Highveld (E Grassland)	3	265
Onitis curvipes (E4)	16.69	458	914	Endemic	Highveld (Grassland) / S Cape	14	150 365
Onitis deceptor (NE6)	19.86	625	961		E Savanna / Kalahari (SW)	62	1 264 130
Onitis fabricii (NE6)	22.05	713	999		E Savanna	22	2 595 525
Onitis fulgidus (NE6)	20.44	633	832		E Savanna	112	366 000
Onitis inversidens (NE6)	22.35	608	545		E Savanna	24	1 704 640
Onitis licitus (E4)	13.7	528	1 619	Endemic	Highveld (S Grassland)	2	105
Onitis longitibialis (E3)	17.55	353	1 222	Endemic	Upper Karoo	1	?
Onitis mendax (NE7)	21.48	628	657		Savanna (E & W)	39	2 759 790
Onitis minutus (E1)	16.89	386	393	Endemic	SW Cape / S Cape (Fynbos)	11	70 125
Onitis mniszechi (E6)	18.66	265	1 236	Endemic	W Savanna - N Namibia	5	67 800
Onitis obenbergeri (NE6)	22.27	431	533		E Savanna	26	59 050
Onitis obscurus (NE2)	20.40	478	1 299		W Savanna - N Namibia	21	157 030
Onitis orthopus (NE2)	21.38	618	1 056		W Savanna - N Botswana	7	281 070
Onitis paraconfusus (E10)	22.35	578	377	Endemic	E Savanna	2	1 950
Onitis parainflaticollis (E10)	18.25	631	1 115	Endemic	E Savanna / Kalahari	12	116 085
Onitis pecuarius (E4)	16.68	730	876	Endemic	Highveld (E Grassland) / E Savanna / S Cape	116	198 180
Onitis perpunctatus (E4)	16.47	741	1 268	Endemic	Highveld (Grassland) / E Savanna	67	96 210
Onitis picticollis (NE7)	19.71	657	871		Savanna (E & W)	65	327 800

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**Endemic to South Africa, Botswana and/or Namibia; absence of an entry = non-endemic species.
***Does not include type locality.

APPENDIX 3: Summary of average climatic, topographical and distributional data for dung beetle species recorded in South Africa, Botswana and Namibia (continued)

Species/subspecies (Generalised distribution patterns) (See summaries in Table 2)	Average data* (see species accounts for SD)			Endemic status**	Main distribution patterns in RSA, Botswana, Namibia (see Fig. 6, Summary Tables 2, 3, & species accounts)	N 5×5 km² polygons*	EOO (km²)
	Annual temperature (°C)	Annual rainfall (mm)	Altitude (m)				
Tribe ONITINI (Fig. 6J) (continued)							
Onitis pseudosetosus (NE6)	19.38	639	1 063		E Savanna	18	191 355
Onitis robustus (NE7)	22.19	697	691		Savanna (E & W)	15	3 525 050
Onitis setosus (NE2)	19.19	417	1 131		W Savanna - N Namibia	8	119 160
Onitis tortuosus (NE1)	16.98	751	1 248		Highveld (Grassland) / E Savanna	204	348 320
Onitis uncinatus (NE7)	19.79	599	1 015		Savanna (E & W)	313	4 665 140
Onitis viridulus (NE6)	20.20	715	803		E Savanna	206	4 084 025
Onitis westermanni (NE6)	20.48	655	954		E Savanna	48	944 160
Platyonitis bicuariensis (NE2)	22.23	609	1 092		W Savanna - N Namibia	3	88 760
Tropidonitis paradoxus (NE3)	22.45	720	36		NE Coast - KZN	6	2 455
Tribe ONTHOPHAGINI (Figs 6K, 6L, 6M)							
Caccobiomorphus megaponerae (NE6)	22.06	600	703		E Savanna	7	299 670
Caccobius castaneus (NE7)	21.18	494	863		Savanna (E & W)	12	2 314 560
Caccobius cavatus (NE6)	21.36	693	539		E Savanna / NE Coast - KZN	26	861 245
Caccobius ferrugineus (NE7)	20.37	510	951		Savanna (E & W) / Kalahari	137	4 823 540
Caccobius histerinus (NE6)	21.25	696	473		E Savanna	38	1 133 180
Caccobius nigritulus (NE7)	21.11	598	695		Savanna (E & W) / Kalahari	102	2 013 940
Caccobius obtusus (NE1)	16.62	796	1 047		Highveld (E Grassland) / S Cape	75	781 120
Cleptocaccobus convexifrons (NE6)	20.95	622	806		E Savanna	12	3 973 335
Cleptocaccobus postlutatus (NE7)	18.90	724	885		Savanna (E & W)	51	1 627 025
Cleptocaccobius viridicollis (NE7)	19.06	448	971		Savanna (E & W) / Kalahari	134	1 295 810
Digitonthophagus gazella (NE6)	19.52	626	804		E Savanna	404	3 711 400
Digitonthophagus namaquensis (NE5)	18.32	215	984		SW Arid (Nama Karoo, Arid W Savanna)	69	795 870
Digitonthophagus viridicollis (NE2)	19.56	390	1 222		W Savanna - N Namibia	29	419 910
Euonthophagus carbonarius (NE6)	21.25	619	627		E Savanna	115	946 605
Euonthophagus flavimargo (E8)	19.30	264	1 080	Endemic	Kalahari (SW)	114	211 965
Euonthophagus jeanneli (NE6)	22.37	582	371		E Savanna	19	409 200
Euonthophagus vicarius (E3)	15.80	282	1 236	Endemic	Upper Karoo	64	97 405
Hamonthophagus acutus (E9)	19.08	219	1 005	Endemic	SW Arid (Nama Karoo) / Kalahari (SW)	50	390 575
Hamonthophagus depressus (NE7)	20.11	676	701		Savanna (E & W)	128	669 355
Hamonthophagus fallax (NE2)	22.50	666	884		W Savanna - N Botswana	7	327 565
Haroldius convexus (E10)	17.20	699	1 452	Endemic	E Savanna	1	?
Heteroclitopus remipes (NE6)	18.99	756	809		E Savanna / E Coast	6	42 635

Species/subspecies (Generalised distribution patterns) (See summaries in Table 2)	Average data* (see species accounts for SD)			Endemic status**	Main distribution patterns in RSA, Botswana, Namibia (see Fig. 6, Summary Tables 2, 3, & species accounts)	N 5×5 km² polygons*	EOO (km²)
	Annual temperature (°C)	Annual rainfall (mm)	Altitude (m)				
Hyalonthophagus alcyon (NE7)	21.91	635	938		Savanna (E & W)	12	474 810
Hyalonthophagus alcyonides (NE6)	20.89	694	576		E Savanna	62	232 385
Kurtops quadraticeps (NE4)	19.81	321	1 079		Kalahari	115	799 195
Kurtops signatus (NE4)	19.81	362	965		Kalahari / E Savanna / Upper Karoo	293	1 133 835
Milichus apicalis (NE7)	21.55	657	509		Savanna (E & W)	32	7 382 875
Mimonthophagus ambiguus (NE3)	22.06	857	34		E Coast	31	298 230
Mimonthophagus anomalus (NE6)	22.68	647	730		E Savanna	22	658 380
Mimonthophagus limbibasis (NE6)	21.55	540	1 044		E Savanna	3	2 790
Onthophagus absyrtus (E4)	15.53	759	1 556	Endemic	Highveld (Grassland)	11	65 350
Onthophagus aequepubens (NE7)	20.50	570	780		Savanna (E & W)	25	245 690
Onthophagus aeruginosus (NE7)	19.43	664	936		Savanna (E & W) / Highveld (Grassland)	232	4 968 210
Onthophagus albipennis (E3)	16.99	245	1 158	Endemic	Upper Karoo	113	126 235
Onthophagus albipodex (NE6)	19.63	686	988		E Savanna	37	324 950
Onthophagus apiciosus (NE6)	19.15	709	1 038		E Savanna	33	2 057 540
Onthophagus asperulus (E4)	16.01	779	1 241	Endemic	Highveld (Grassland)	139	170 285
Onthophagus axillaris (NE2)	18.77	415	1 249		W Savanna - N Namibia	23	393 675
Onthophagus bayeri (E6)	17.58	240	1 520	Endemic	W Savanna - N Namibia	8	10 885
Onthophagus beiranus (NE3)	22.32	887	154		NE Coast - KZN / E Savanna	47	98 720
Onthophagus bicavifrons (NE7)	19.57	633	928		Savanna (E & W)	149	4 290 470
Onthophagus binodis (E4)	15.85	669	1 092	Endemic	Highveld (Grassland) / S Cape	160	274 485
Onthophagus bovinus (NE7)	19.77	416	1 093		Savanna (E & W) / Upper Karoo / Kalahari (SW)	32	642 681
Onthophagus cameloides (E1)	16.78	237	506	Endemic	SW & S Cape (Fynbos, S Karoo) / Upper Karoo	97	241 800
Onthophagus cinctipennis (NE1)	17.62	761	1 240		Highveld (Grassland) / E Savanna	35	217 320
Onthophagus cineraceus (E1)	14.43	473	571	Endemic	SW Cape (Fynbos)	2	180
Onthophagus convexus (NE4)	19.25	279	1 015		Kalahari / Upper Karoo	183	988 530
Onthophagus corniculiger (NE6)	21.68	629	450		E Savanna	14	145 035
Onthophagus cretus (E7)	18.03	876	586	Endemic	E Coast (Forest)	21	44 150
Onthophagus cribripennis (NE6)	17.46	800	1 122		E Savanna / Highveld (E Grassland)	146	206 820
Onthophagus croesulus (E10)	18.43	680	1 113	Endemic	E Savanna / Highveld (E Grassland)	13	128 590
Onthophagus cupricollis (E10)	17.59	762	1 228	Endemic	E Savanna	11	26 645
Onthophagus cyaneoniger (E4)	16.07	590	1 411	Endemic	Highveld (Grassland)	42	181 630
Onthophagus deterrens (E4)	16.62	793	1 275	Endemic	Highveld (Grassland) / E Savanna	55	293 940

*Average data for total 5×5 km2 polygons occupied in Africa south of 15°S.
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APPENDIX 3: Summary of average climatic, topographical and distributional data for dung beetle species recorded in South Africa, Botswana and Namibia (continued)

Species/subspecies (Generalised distribution patterns) (See summaries in Table 2)	Average data* (see species accounts for SD)			Endemic status**	Main distribution patterns in RSA, Botswana, Namibia (see Fig. 6, Summary Tables 2, 3, & species accounts)	N 5×5 km² polygons*	EOO (km²)
	Annual temperature (°C)	Annual rainfall (mm)	Altitude (m)				
Tribe ONTHOPHAGINI (Figs 6K, 6L, 6M) (continued)							
Onthophagus discretus (NE6)	18.96	648	1 166		E Savanna	13	42 255
Onthophagus ebenicolor (NE7)	20.77	619	716		Savanna (E & W)	69	1 691 195
Onthophagus ebenus (NE6)	19.25	704	953		E Savanna / Highveld (N Grassland)	123	847 490
Onthophagus fimetarius (NE7)	18.79	683	1 069		Savanna (E & W) / Highveld (N Grassland)	199	5 546 895
Onthophagus flavolimbatus (NE7)	21.32	627	620		Savanna (E & W)	72	860 785
Onthophagus fritschi (E3)	15.38	413	1 333	Endemic	Upper Karoo	80	174 610
Onthophagus fugitivus (E10)	19.18	607	1 042	Endemic	E Savanna	18	118 900
Onthophagus giraffa (E1)	15.78	408	480	Endemic	SW Cape / S Cape (Fynbos)	52	59 495
Onthophagus giuseppecarpanetoi (NE3)	22.26	754	36		NE Coast - KZN	27	8 945
Onthophagus gonopygus (NE2)	16.99	185	881		W Savanna - Arid W Namibia	17	102 535
Onthophagus granulifer (NE4)	19.65	299	1 060		Kalahari	127	1 080 205
Onthophagus graphicus (NE7)	19.96	486	935		Savanna (E & W)	9	1 088 955
Onthophagus herus (NE6)	23.32	722	439		E Savanna	8	1 168 730
Onthophagus hyaena (E4)	15.18	614	1 250	Endemic	Highveld (S Grassland) / S Cape	38	38 760
Onthophagus immundus (E1)	16.02	340	521	Endemic	SW Cape / S Cape (Fynbos)	13	26 615
Onthophagus interstitialis (E4)	17.85	653	1 042	Endemic	Highveld (N Grassland) / E Savanna	95	251 810
Onthophagus juvencus (NE3)	22.54	865	67		NE Coast - KZN / E Savanna	25	2 971 515
Onthophagus kochi (E6)	20.41	442	949	Endemic	W Savanna - N Namibia / N Botswana	7	42 635
Onthophagus lacustris (NE3)	22.33	846	245		NE Coast - KZN / E Savanna	38	874 260
Onthophagus lamelliger (NE6)	21.68	593	591		E Savanna	107	1 440 975
Onthophagus lamnifer (E4)	15.90	691	1 429	Endemic	Highveld (NE Grassland)	38	96 245
Onthophagus leroyi (NE6)	21.77	612	382		E Savanna	27	228 595
Onthophagus leucopygus (NE4)	18.78	381	1 224		Kalahari	35	587 600
Onthophagus lugubris (E4)	14.90	719	1 429	Endemic	Highveld (Grassland)	47	180 110
Onthophagus minutus (E1)	16.61	303	118	Endemic	SW Cape / S Cape (Fynbos)	39	44 485
Onthophagus monodon (E4)	16.29	753	1 416	Endemic	Highveld (Grassland)	16	100 835
Onthophagus naso (E7)	18.48	833	578	Endemic	Highveld (Grassland) / E Savanna / E Coast	18	70 340
Onthophagus obtusicornis (NE7)	19.03	634	1 014		Savanna (E & W) / Highveld (Grassland)	179	418 675
Onthophagus obtutus (E4)	14.99	677	1 579	Endemic	Highveld (Grassland)	33	89 365
Onthophagus pallidipennis (NE6)	20.11	502	947		E Savanna / Kalahari	97	1 056 735
Onthophagus parumnotatus (NE6)	17.48	812	1 213		E Savanna / Highveld (Grassland)	103	2 391 165
Onthophagus pauxillus (NE6)	19.34	657	949		E Savanna	67	316 415

Species/subspecies (Generalised distribution patterns) (See summaries in Table 2)	Average data* (see species accounts for SD)			Endemic status**	Main distribution patterns in RSA, Botswana, Namibia (see Fig. 6, Summary Tables 2, 3, & species accounts)	N 5×5 km² polygons*	EOO (km²)
	Annual temperature (°C)	Annual rainfall (mm)	Altitude (m)				
Onthophagus pellax (E10)	19.06	591	1 151	Endemic	E Savanna	24	40 975
Onthophagius peringueyi (E3)	17.00	247	1 157	Endemic	Upper Karoo	136	219 865
Onthophagus pilosus (E4)	16.16	757	1 353	Endemic	Highveld (Grassland) / E Savanna	51	156 440
Onthophagus plebejus (NE7)	22.63	619	654		Savanna (E & W)	32	1 949 910
Onthophagus probus (NE5)	18.76	205	1 010		SW Arid (Nama Karoo, Arid W Savanna)	218	830 525
Onthophagus producticollis (NE6)	17.53	719	1 283		E Savanna	18	85 445
Onthophagus pugionatus (NE6)	19.31	714	916		E Savanna / Highveld (Grassland)	129	4 391 285
Onthophagus pullus (NE7)	20.09	636	852		Savanna (E & W)	46	2 692 290
Onthophagus quadrimaculatus (NE7)	20.33	618	827		Savanna (E & W)	34	1 875 455
Onthophagus quadrinodosus (NE6)	19.54	676	955		E Savanna	52	2 016 665
Onthophagus rasipennis (NE6)	20.02	655	811		E Savanna	73	230 805
Onthophagus scapularis (E2)	17.55	493	233	Endemic	S Cape (Albany Thicket)	2	1 725
Onthophagus semiflavus (NE5)	19.04	210	966		SW Arid (Kalahari (SW), Nama Karoo)	109	226 630
Onthophagus suffusus (NE7)	21.84	586	719		Savanna (E & W)	31	962 255
Onthophagus tricorniger (E9)	19.18	333	1 430	Endemic	SW Arid (Arid W Savanna)	6	65 590
Onthophagus trinodosus (E10)	19.24	635	1 020	Endemic	E Savanna	14	32 470
Onthophagus ursinus (NE3)	22.22	861	39		NE Coast - KZN	17	38 715
Onthophagus variolosus (E4)	15.68	519	820	Endemic	Highveld (S Grassland) / S Cape	16	58 525
Onthophagus venustulus (NE4)	19.57	329	1 084		Kalahari	184	1 414 010
Onthophagus verticalis (NE6)	20.20	520	1 045		E Savanna / Kalahari	65	1 288 690
Onthophagus vigens (E4)	15.44	834	1 367	Endemic	Highveld (E Grassland)	44	61 695
Onthophagus vinctus (NE7)	20.16	663	797		Savanna (E & W)	305	8 771 775
Onthophagus virescens (NE6)	22.61	651	572		E Savanna	14	137 725
Onthophagus vylderi (E8)	20.81	588	1 050	Endemic	Kalahari	8	241 110
Phalops ardea (NE7)	21.53	618	662		Savanna (E & W)	97	1 179 470
Phalops boschas (NE6)	21.10	630	724		E Savanna	130	2 069 530
Phalops bubalus (E4)	15.59	527	1 256	Endemic	Highveld (Grassland) / Upper Karoo	108	355 495
Phalops dregei (NE7)	17.93	431	1 102		Savanna (E & W) / Upper Karoo	178	500 430
Phalops flavocinctus (NE6)	20.55	677	716		E Savanna	156	1 564 855
Phalops pauliani (E6)	19.90	400	1 437	Endemic	W Savanna - N Namibia	11	66 480
Phalops plancus (NE2)	17.00	232	885		W Savanna - Arid W Namibia	14	39 635
Phalops prasinus (NE2)	18.53	324	1 203		W Savanna - N Namibia	32	115 340

*Average data for total 5×5 km2 polygons occupied in Africa south of 15°S.
**Endemic to South Africa, Botswana and/or Namibia; absence of an entry = non-endemic species.
***Does not include type locality.

APPENDIX 3: Summary of average climatic, topographical and distributional data for dung beetle species recorded in South Africa, Botswana and Namibia (continued)

Species/subspecies (Generalised distribution patterns) (See summaries in Table 2)	Average data* (see species accounts for SD)			Endemic status**	Main distribution patterns in RSA, Botswana, Namibia (see Fig. 6, Summary Tables 2, 3, & species accounts)	N 5×5 km² polygons*	EOO (km²)
	Annual temperature (°C)	Annual rainfall (mm)	Altitude (m)				
Tribe ONTHOPHAGINI (Figs 6K, 6L, 6M) (continued)							
Phalops pyroides (E9)	18.71	242	1 133	Endemic	SW Arid (Nama Karoo, Arid W Savanna)	61	122 540
Phalops rufosignatus (NE5)	18.63	311	1 161		SW Arid (Nama Karoo, Arid W Savanna)	76	591 895
Phalops smaragdinus (NE6)	20.36	731	825		E Savanna	107	1 479 555
Phalops wittei (NE4)	19.18	300	1 102		Kalahari / Upper Karoo / Highveld (Grassland)	254	1 562 330
Phalops zuninoi (NE2)	21.83	674	1 158		W Savanna - N Namibia	2	197 250
Proagoderus aciculatus (NE3)	21.76	862	43		E Coast	74	33 450
Proagoderus aureiceps (NE3)	21.97	763	157		E Savanna / NE Coast - KZN	63	192 750
Proagoderus bicallosus (NE6)	22.27	656	517		E Savanna	52	3 227 420
Proagoderus chalcostolus (NE1)	17.99	829	1 026		Highveld (Grassland) / E Savanna	136	232 570
Proagoderus dives (NE3)	22.05	805	411		E Savanna / NE Coast - KZN	57	1 444 830
Proagoderus furcifer (NE7)	22.20	555	951		Savanna (E & W)	7	267 405
Proagoderus lanista (E4)	17.67	672	1 193	Endemic	Highveld (Grassland) / W Savanna - N Namibia	63	300 285
Proagoderus loricatus (NE6)	21.42	604	595		E Savanna	51	1 895 725
Proagoderus plato (NE2)	21.63	613	1 023		W Savanna - N Namibia / N Botswana	2	235 670
Proagoderus quadrituber (NE3)	21.58	858	315		E Savanna	11	134 250
Proagoderus rangifer (NE6)	21.86	598	586		E Savanna	35	1 303 445
Proagoderus rectefurcatus (NE6)	22.51	580	630		E Savanna	20	847 660
Proagoderus sapphirinus (NE4)	19.56	411	1 111		Kalahari / E Savanna	131	1 117 105
Proagoderus tersidorsis (E10)	20.69	697	532	Endemic	E Savanna	74	85 690
Tribe SCARABAEINI (Figs 6N, 6O)							
Escarabaeus remii (E6)	22.38	503	937	Endemic	W Savanna - N Botswana	9	74 550
Escarabaeus satyrus (NE5)	18.17	230	1 017		SW Arid (Nama Karoo, W Savanna, Kalahari)	342	1 491 750
Kheper bonellii (E1)	17.07	223	162	Endemic	SW Cape - West Coast (Fynbos, Succ. Karoo)	36	25 000
Kheper clericus (E7)	21.18	833	161	Endemic	NE Coast - KZN - E Savanna	5	750
Kheper cupreus (NE7)	21.04	487	866		Savanna (E & W)	59	1 865 025
Kheper kalaharicus (E8)	20.42	209	953	Endemic	Kalahari (SW)	6	6 000
Kheper lamarcki (NE4)	20.67	548	849		Kalahari / E Savanna / NE Coast - KZN	153	2 173 065
Kheper nigroaeneus (NE6)	20.07	672	840		E Savanna	207	662 125
Kheper prodigiosus (NE4)	21.32	484	891		Kalahari / E Savanna	77	2 045 625
Kheper subaeneus (NE6)	20.77	641	750		E Savanna	88	1 257 850
Kheper vethi (NE2)	16.93	193	519		W Savanna - Arid NW Namibia	2	35 400
Kheper zurstrasseni (E4)	18.22	626	1 206	Endemic	Highveld (N Grassland) / E Savanna	3	1 450

Species/subspecies (Generalised distribution patterns) (See summaries in Table 2)	Average data* (see species accounts for SD)			Endemic status**	Main distribution patterns in RSA, Botswana, Namibia (see Fig. 6, Summary Tables 2, 3, & species accounts)	N 5×5 km² polygons*	EOO (km²)
	Annual temperature (°C)	Annual rainfall (mm)	Altitude (m)				
Pachylomera femoralis (NE4)	20.94	583	796		E Savanna / Kalahari / NE Coast - KZN	197	2 663 660
Pachylomera opacus (NE4)	19.30	275	1 076		Kalahari / Upper Karoo	78	800 000
Pachysoma aesculapius (E1)	17.05	259	134	Endemic	SW Cape - West Coast (Fynbos)	26	10 750
Pachysoma bennigseni (E1)	15.53	41	287	Endemic	SW Cape - Namaqualand / Namib (Succ. Karoo)	24	8 500
Pachysoma denticolle (E5)	16.11	45	578	Endemic	SW Arid - Namib Desert	58	40 000
Pachysoma endroedyi (E1)	18.22	156	91	Endemic	SW Cape - Namaqualand (Succulent Karoo)	12	130
Pachysoma fitzsimonsi (E5)	15.56	83	1 010	Endemic	SW Arid - Namib Desert	13	8 250
Pachysoma gariepinum (E1)	15.63	57	397	Endemic	SW Cape - Namaqualand / Namib (Succ. Karoo)	79	17 650
Pachysoma glentoni (E1)	17.91	191	136	Endemic	SW Cape - Namaqualand (Succulent Karoo)	9	700
Pachysoma hippocrates (E1)	17.05	166	96	Endemic	SW Cape - West Coast (Succ. Karoo, Fynbos)	64	8 500
Pachysoma rodriguesi (E5)	16.16	40	555	Endemic	SW Arid - Namib Desert	44	24 000
Pachysoma rotundigena (E5)	16.06	89	1 021	Endemic	SW Arid - Namib Desert	18	9 500
Pachysoma schinzi (E5)	14.02	89	1 397	Endemic	SW Arid - S Namibia (Nama Karoo, Desert)	9	1 400
Pachysoma striatum (E1)	17.29	114	113	Endemic	SW Cape - Namaqualand (Succulent Karoo)	85	6 000
Pachysoma valeflorae (E5)	15.20	30	388	Endemic	SW Arid - Namib Desert (Succulent Karoo)	3	200
Scarabaeolus afronitidus (E8)	20.47	347	1 004	Endemic	Kalahari (SW)	3	9 250
Scarabaeolus anderseni (E8)	19.81	321	1 070	Endemic	Kalahari	55	627 900
Scarabaeolus andreaei (NE3)	23.58	835	83		NE Coast / E Savanna	6	34 050
Scarabaeolus bohemani (NE7)	17.98	332	1 141		Savanna (E & W) / Upper Karoo	290	1 063 280
Scarabaeolus canaliculatus (E5)	15.25	67	894	Endemic	SW Arid - Namib Desert	2	910
Scarabaeolus carniphilus (E8)	19.40	334	1 135	Endemic	Kalahari (SW)	3	4 285
Scarabaeolus clanceyi (NE3)	22.28	673	167		NE Coast / E Savanna	14	20 500
Scarabaeolus damarensis (E8)	19.65	297	1 078	Endemic	Kalahari	113	952 000
Scarabaeolus flavicornis (NE4)	19.12	272	988		Kalahari / SW Cape - Namaqualand (Succ. Karoo)	178	844 500
Scarabaeolus fritschi (E9)	17.63	192	1 047	Endemic	SW Arid (Nama Karoo)	63	110 000
Scarabaeolus gracai (NE3)	23.10	615	337		NE Coast / E Savanna	4	3 040
Scarabaeolus inoportunus (E8)	19.38	257	1 055	Endemic	Kalahari (SW)	67	510 500
Scarabaeolus inquisitus (E4)	18.89	390	1 141	Endemic	Kalahari / Nama Karoo	22	446 500
Scarabaeolus intricatus (E1)	17.09	233	224	Endemic	SW Cape (Fynbos, Succulent Karoo)	69	48 000
Scarabaeolus karrooensis (E9)	18.46	210	1 019	Endemic	SW Arid (Nama Karoo)	45	359 300
Scarabaeolus kochi (E8)	19.05	274	1 094	Endemic	Kalahari (SW)	53	430 000
Scarabaeolus lucidulus (NE4)	20.90	559	1 020		Kalahari (N) / E Savanna	12	382 950

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***Does not include type locality.

APPENDIX 3: Summary of average climatic, topographical and distributional data for dung beetle species recorded in South Africa, Botswana and Namibia (continued)

Species/subspecies (Generalised distribution patterns) (See summaries in Table 2)	Average data* (see species accounts for SD)			Endemic status**	Main distribution patterns in RSA, Botswana, Namibia (see Fig. 6, Summary Tables 2, 3, & species accounts)	N 5×5 km² polygons*	EOO (km²)
	Annual temperature (°C)	Annual rainfall (mm)	Altitude (m)				
Tribe SCARABAEINI (Figs 6N, 6O) (continued)							
Scarabaeolus megaparvulus (E9)	17.05	177	1 083	Endemic	SW Arid (Nama Karoo)	40	59 650
Scarabaeolus namibensis (NE2)	16.69	60	577		SW Arid - Namib Desert	15	27 000
Scarabaeolus niemandi (E10)	19.63	521	1 006	Endemic	E Savanna	5	4 395
Scarabaeolus obsoletepunctatus (NE2)	16.90	228	559		W Savanna - Arid NW Namibia	1	7 205
Scarabaeolus pabulator (E9)	18.79	168	941	Endemic	SW Arid (Nama Karoo)	40	247 150
Scarabaeolus parvulus (NE5)	18.54	196	991		SW Arid (Nama Karoo, Kalahari (SW), Namib)	108	398 100
Scarabaeolus planipennis (NE3)	22.54	685	92		NE Coast / E Savanna	12	4 900
Scarabaeolus reichei (E1)	17.72	170	99	Endemic	SW Cape - West Coast (Fynbos, Succ. Karoo)	58	12 500
Scarabaeolus rubripennis (E5)	16.01	56	594	Endemic	SW Arid - Namib Desert / Succulent Karoo	35	55 500
Scarabaeolus soutpansbergensis (E10)	21.18	434	741	Endemic	E Savanna	10	5 100
Scarabaeus alienus (E1)	17.20	65	574	Endemic	SW Cape - Namaqualand / Namib Desert	3	18 000
Scarabaeus ambiguus (E4)	18.02	509	1 323	Endemic	Highveld (Grassland) / Savanna (E & W)	106	371 530
Scarabaeus basuto (E4)	14.81	455	1 460	Endemic	Highveld (Grassland) / Upper Karoo	63	134 360
Scarabaeus bornemisszai (NE3)	22.01	875	12		NE Coast - KZN (Forest)	23	3 250
Scarabaeus caffer (E4)	16.74	891	1 214	Endemic	Highveld (E Grassland)	29	70 500
Scarabaeus cognatus (E6)	17.66	77	531	Endemic	W Savanna - Arid NW Namibia	5	18 345
Scarabaeus convexus / spretus (E4)	16.13	629	680	Endemic	Highveld (E Grassland) / E Coast / S & SW Cape	9	45 980
Scarabaeus costatus (E9)	18.87	225	1 023	Endemic	SW Arid (Kalahari (SW), Nama Karoo, Namib)	73	298 810
Scarabaeus deludens (E10)	20.44	610	795	Endemic	E Savanna / N Namibia	40	186 900
Scarabaeus ebenus (NE3)	22.49	672	301		NE Coast - KZN / E Savanna	20	422 865
Scarabaeus funebris (E4)	18.93	538	1 135	Endemic	Highveld (N Grassland) / Savanna (E & W)	22	104 390
Scarabaeus galenus (NE7)	20.59	630	750		Savanna (E & W)		699 090
Scarabaeus geminogalenus (NE3)	21.83	652	380		NE Coast - KZN / E Savanna	16	40 770
Scarabaeus goryi (NE4)	20.50	593	807		E Savanna	136	2 990 240
Scarabaeus heqvisti (E4)	18.75	652	1 173	Endemic	Highveld (N Grassland)	3	305
Scarabaeus hottentorum (E1)	17.57	126	564	Endemic	SW Cape - Namaqualand (Succulent Karoo)	7	3 335
Scarabaeus interstitialis (NE6)	18.75	584	1 151		E Savanna	43	119 975
Scarabaeus karae (E4)	16.90	676	1 447	Endemic	Highveld (NW Grassland)	3	3080
Scarabaeus piliventris (E1)	17.76	181	295	Endemic	SW Cape - West Coast (Fynbos, Succ. Karoo)	6	3 305
Scarabaeus proboscideus (E8)	18.81	219	808	Endemic	Kalahari (SW) / SW Cape - W Coast (S Karoo)	222	502 100
Scarabaeus proximus (E1)	15.85	62	274	Endemic	SW Cape - Namaqualand / Namib (Succ. Karoo)	24	16 030
Scarabaeus rugosus (E1)	17.23	186	98	Endemic	SW Cape - West Coast (Fynbos, Succ. Karoo)	86	11 000

Species/subspecies (Generalised distribution patterns) (See summaries in Table 2)	Average data* (see species accounts for SD)			Endemic status**	Main distribution patterns in RSA, Botswana, Namibia (see Fig. 6, Summary Tables 2, 3, & species accounts)	N 5×5 km² polygons*	EOO (km²)
	Annual temperature (°C)	Annual rainfall (mm)	Altitude (m)				
Scarabaeus rusticus (E10)	18.25	681	1 228	Endemic	E Savanna / Highveld (N Grassland)	156	105 335
Scarabaeus savignyi (E2)	16.76	455	388	Endemic	S Cape (Fynbos, Albany Thicket)	7	31 775
Scarabaeus schulzae (E10)	19.41	564	1 016	Endemic	E Savanna	13	2 500
Scarabaeus suri (E1)	16.69	276	214	Endemic	SW Cape (Fynbos)	38	23 250
Scarabaeus viator (E3)	17.04	252	1 135	Endemic	Upper Karoo	169	288 635
Scarabaeus vicinus (E8)	17.91	309	1 180	Endemic	Kalahari (SW) / Upper Karoo	74	791 785
Scarabaeus westwoodi (E4)	11.06	830	2 155	Endemic	Highveld (NE Grassland)	8	18 000
Scarabaeus zambesianus (NE4)	20.71	445	947		E Savanna / Kalahari (NE)	100	579 415
Sceliages adamastor (E1)	17.32	337	339	Endemic	S & SW Cape (Fynbos) / Upper Karoo	8	174 095
Sceliages brittoni (E1)	17.21	199	100	Endemic	SW Cape - West Coast (Fynbos, Succ. Karoo)	17	6 180
Sceliages difficilis (NE6)	17.95	734	1 206		E Savanna / Highveld (NE Grassand)	41	214 130
Sceliages gagates (NE3)	22.43	778	31		NE Coast - KZN	11	13 335
Sceliages granulatus (E8)	18.91	352	1 167	Endemic	Kalahari (SW)	7	109 200
Sceliages hippias (E10)	17.86	680	1 302	Endemic	E Savanna	41	103 400
Tribe SISYPHINI (Fig. 6P)							
Neosisyphus barbarossa (E4)	14.73	682	1 408	Endemic	Highveld (E Grassland) / S Cape	23	27 150
Neosisyphus calcaratus (NE6)	21.02	612	744		E Savanna	86	712 200
Neosisyphus confrater (NE6)	19.68	892	687		E Savanna / NE Coast / Highveld (E Grassland)	50	118 955
Neosisyphus fortuitus (NE6)	19.81	746	748		E Savanna	56	154 350
Neosisyphus infuscatus (NE6)	21.18	687	431		E Savanna	56	900 785
Neosisyphus kuehni (E4)	14.11	783	1 646	Endemic	Highveld (E Grassland))	8	30 620
Neosisyphus macrorubrus (E4)	16.82	366	1 295	Endemic	Highveld (W) / Upper Karoo / N Namibia	129	239 965
Neosisyphus mirabilis (NE3)	21.74	825	42		E Coast / E Savanna	35	14 150
Neosisyphus quadricollis (E1)	15.73	298	552	Endemic	SW Cape - West Coast (Fynbos) / Upper Karoo	8	25 800
Neosisyphus rubrus (NE6)	18.33	704	1 067		E Savanna / Highveld (Grassland)	299	720 705
Neosisyphus spinipes (NE6)	20.16	823	484		E Savanna / E Coast	126	1 156 170
Sisyphus alveatus (NE2)	22.60	541	919		W Savanna - N Botswana	1	1 801 180
Sisyphus caffer (E4)	16.53	674	1 260	Endemic	Highveld (Grassland)	71	31 865
Sisyphus costatus (E4)	15.75	788	1 326	Endemic	Highveld (Grassland) / S Cape	45	142 520
Sisyphus fasciculatus (NE3)	19.12	837	755		NE Coast - KZN / E Savanna (Forest)	31	50 820
Sisyphus goryi (NE7)	20.11	666	906		Savanna (E & W)	214	5 042 590
Sisyphus impressipennis (NE7)	20.04	693	987		Savanna (E & W)	59	2 175 705

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Species/subspecies (Generalised distribution patterns) (See summaries in Table 2)	Average data* (see species accounts for SD)			Endemic status**	Main distribution patterns in RSA, Botswana, Namibia (see Fig. 6, Summary Tables 2, 3, & species accounts)	N 5×5 km² polygons*	EOO (km²)
	Annual temperature (°C)	Annual rainfall (mm)	Altitude (m)				
Tribe SISYPHINI (Fig. 6P) (continued)							
Sisyphus manni (E10)	17.95	749	1 126	Endemic	E Savanna / Highveld (N Grassland)	45	124 410
Sisyphus muricatus (E4)	15.52	709	1 094	Endemic	Highveld (E Grassland) / S Cape	28	24 500
Sisyphus nanniscus (NE6)	20.65	811	523		E Savanna / NE Coast - KZN	74	919 450
Sisyphus neobornemisszanus (NE3)	22.28	844	8		NE Coast - KZN	22	4 500
Sisyphus oralensis (NE3)	21.99	853	28		NE Coast - KZN	32	18 105
Sisyphus perissinottoi (E2)	16.44	353	608	Endemic	S Cape (Albany Thicket, Fynbos)	4	9 685
Sisyphus sordidus (NE6)	21.99	803	225		E Savanna / NE Coast - KZN	59	326 650
Sisyphus splendidus (NE2)	18.67	563	1 495		W Savanna - N Namibia	3	18 600
Sisyphus umbraphilus (E10)	20.34	744	519	Endemic	E Savanna	4	21 880

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**Endemic to South Africa, Botswana and/or Namibia; absence of an entry = non-endemic species.
***Does not include type locality.

REFERENCES

Abdalla, I.H., Deschodt, C.M., Scholtz, C.H. & Sole, C.L. 2018. An update to the taxonomy of the genus *Macroderes* Westwood 1842 (Coleoptera: Scarabaeidae: Scarabaeinae) with descriptions of new species from South Africa. *Zootaxa* 4504: 041–075.

Ádám, L. 2003. Faunisztikai adatok a Karpat-mendenceböl. *Folia Historico Naturalia Musei Matraensis* 27: 101–136.

Ancey, F. 1883. Contributions à la faune de l'Afrique orientale. Descriptions de Coléoptères nouveaux. *Il Naturalista Siciliano* 2: 68–72.

Arrow, G.J. 1900. On a collection of insects and arachnids made in 1895 and 1897, by Mr. C.V.A. Peels, F.Z.S., in Somaliland, with description of new species. Scarabaeidae. *Proceedings of the Zoological Society of London*: 22–25.

Arrow, G.J. 1909. Four new lamellicorn Coleoptera from the Oriental region. *The Annals and Magazine of Natural History, including Zoology, Botany and Geology, London* 8: 91–94.

Arrow, G.J. 1931. *The Fauna of British India, Including Ceylon and Burma. Coleoptera Lamellicornia Part III (Coprinae)*. Taylor and Francis, London, 1–428.

Arrow, G.J. 1933. Notes on Coprid Coleoptera with descriptions of a new genus and a few new species. *The Annals and Magazine of Natural History, including Zoology, Botany and Geology, London* 10: 421–430.

Balthasar, V. 1937. Neue coprophage Scarabaeiden von der Ukerewe-Insel in Ost-Afrika. *Arbeiten uber morphologische und taxonomische Entomologie aus Berlin-Dahlem, Berlin-Dahlem* 4: 192–203.

Balthasar, V. 1938. Neue gattungen und arten der Südamerikanischen Coprophagen. *Entomologische Blätter, Krefeld* 34: 210–223.

Balthasar, V. 1939a. Neue arten der coprophagen Scarabaeiden aus dem Museo Zoologico delle R. Universita di Firenze. *Redia* 25: 1–36.

Balthasar, V. 1939b. Neue Arten der palaearktischen und neotropischen coprophagen Scarabaeiden. Entomologicke Listy. *Brno (Folia entomologica)* 2: 41–47.

Balthasar, V. 1940. Einige neue Scarabaeiden-Arten. *Casopis Ceskoslovenske Spolecnosti Entomologicke* 37: 67–76.

Balthasar, V. 1941a. Eine reihe von neuen coprophagen Scarabaeiden. *Mitteilungen der munchner entomologischen Gesellschaft, Munchen* 31: 164–184.

Balthasar, V. 1941b. Neue coprophage Scarabaeiden des Deutschen Entomologischen Instituts (Coleoptera : Scarabaeidae). 71. Beitrag zur Kenntnis der Scarabaeidae. *Arbeiten über morphologische und taxonomische Entomologie aus Berlin-Dahlem* 8 :181–184.

Balthasar, V. 1942. Neue arten und gattungen der coprophagen scarabaeiden. 75. Beitrag zur kenntnis der Scarabaeiden. *Sbornik entomologickeho oddeleni narodniho Musea v Praze, Praha* 20: 188–206.

Balthasar, V. 1946. Les nouvelles espèces Aethiopiennes du genre *Onthophagus*. *Acta Societatis Entomologicae Cechosloveniae* 43: 15–19.

Balthasar, V. 1956. Einige neue laparosticte Scarabaeiden. 27. Beitrag zur Kenntnis der Scarabaeiden. *Entomologische Blätter, Krefeld* 52: 66.

Balthasar, V. 1958. Eine neue Untergattung und einige neue Arten der Gattung *Copris* Geoffroy. *Acta entomologica Musei nationalis Pragae* 32: 471–480.

Balthasar, V. 1959. Beitrag zur Kenntnis der Gattung *Onthophagus* Latr. *Acta Entomologica Musei Nationalis Pragae*, 33: 461–471.

Balthasar, V. 1961a. Zwei neue Gattungen der Familie Scarabaeidae (Col.). (107. Beitrag zur Kenntnis der Scarabaeidae.). *Entomologische Arbeiten aus dem Museum G. Frey* 12: 174–181.

Balthasar, V. 1961b. Coléoptères Scarabaeidae nouveaux de l'Afrique Tropicale. *Revue de Zoologie et de Botanique africains, Bruxelles* 63: 96–104.

Balthasar, V. 1963a. Neue arten der Scarabaeidae und Aphodiidae aus Asien und Afrika. *Entomologische Blätter* 59: 91–97.

Balthasar, V. 1963b. Eine neue Gattung und neue Arten der Fam. Scarabaeidae. 114. Beitrag zur Kenntnis der Scarabaeoidea. *Revue de Zoologie et de Botanique Africains, Bruxelles* 68: 86–98.

Balthasar, V. 1963c. Neue arten der familie Scarabaeidae. *Acta Societatis Entomologicae Cechosloveniae* 60: 284–295.

Balthasar, V. 1963d. Monographie der Scarabeidae und Aphodiidae der palaearktischen und orientalischen Region (Coleoptera: Lamellicornia). Band 2. Coprinae (Onitini, Oonticellini, Onthophagini). Verlag der Tschechoslowakischen Akademie der Wissenschaften, Prague: pp 627.

Balthasar, V. 1963e. Exploration du Parc National de la Garamba. Oniticellini. Eine neue art von *Drepanocerus*. *Institut des Parcs Nationaux du Congo et du Rwanda. Mission H. de Saeger (1949-1952)* 40: 131–135.

Balthasar, V. 1964a. Neue Oniticellinen-Arten. 119. Beitrag zür Kenntnis der Scarabaeoidea. *Beitrage zur Entomologie, Berlin* 14: 619–624.

Balthasar, V. 1964b. *Caccobiomorphus*, eine neue Gattung der Pinotini. *Entomologische Blätter, Krefeld* 60: 31–33.

Balthasar, V. 1965a. Eine neue undergattung und neue arten der familie Scarabaeidae (121. Beitrag zur Kenntnis der Scarabaeoidea). *Acta entomologica bohemoslovaca* 62: 14–23.

Balthasar, V. 1965b. Monographie der untergattung *Metacatharsius* Paulian. *Entomologische Abhandlungen Staatlichen Museum für Tierkunde, Dresden* 31: 1–48.

Balthasar, V. 1968. Neue Scarabaeiden Arten. *Beitrage zur Entomologie, Berlin* 18: 953–958.

Balthasar, V. 1970. Neue Arten der Scarabaeoidea. *Acta Entomologica Bohemoslovaca, Praha* 67: 245–253.

Barbero, E., Palestrini, C. & Roggero, A. 1998. Phylogenetic relationships in the genus *Scarabaeus* Linnaeus. Atti 1. Colloquio Nazionale di Sistematica Cladistica. Memorie del Museo civico di storia naturale di Verona (2), *Sezione Scienze della Vita* 13: 87–96.

Barbero, E., Palestrini, C. & Roggero, A. 2003. Revision of the genus *Phalops*. *Museo Regionale di Scienze Naturale Torino Monografia* 38: 1–378.

Barbero, E., Palestrini, C. & Roggero, A. 2009a. Systematics and phylogeny of *Eodrepanus*, a new Drepanocerine genus, with comments on biogeographical data. *Journal of Natural History* 43: 1835–1878.

Barbero, E., Palestrini, C. & Roggero, A. 2009b. Taxonomic study of *Drepanellus* gen. n., with the description of two new species. *Deutsche Entomologische Zeitschrift* 56: 251–265.

Barbero, E., Palestrini, C. & Zunino, M. 1991. Filogenesi, biogeografia e sistematica generica dei Sisyphini (Coleoptera: Scarabaeidae). *16° Congresso Nazionale Italiano di Entomologia* 1: 837–844.

Bates, H.W. 1868. Notes on genera and species of Copridae. *Coleopterologische Hefte* 4: 87–91.

Bates, H.W. 1887. Biologia Central Americana, Zoologia, Insecta, Coleoptera, Pectinicornia, Lamellicornia (1887–1889). Godman F.D. & Salvin O. (Editors) 2: 1–432.

Bates, H.W. 1888. Tropical african Coleoptera chiefly from the Zanzibar mainland. *Entomologist's Monthly Magazine, London* 24: 237–242.

Bedel, L. 1892a. Synopsis des *Chironitis*, *Onitis* et *Bubas* de la région méditerranéenne. *L'Abeille, Paris* 27: 250–280.

Bedel, L. 1892b. Revision des *Scarabaeus* paléarctiques. *L'Abeille, Paris* 27: 281–288.

Bertolini, J. 1849. Illustratio rerum naturalium Mozambici. Dissertatio 1 de Coleopteris. Novi Commentarii. *Academiae Scientiarum Instituti Bononiensis* 10: 381–434.

Bertolini, J. 1855. Illustratio rerum naturalium Mozambico. Coleoptera. *Memorie della Reale Accademia delle Scienze dell'Istituto di Bologna, Classe di Scienze Fisiche* 6: 419–446.

Bezdek, A. & Sladecek, F.X.J. 2012. *Platyonitis oberthueri* Janssens, 1942 and *Epionitis tarsatus* Balthasar, 1942 – synonymy confirmed. *Zootaxa* 3267: 65–68.

Biswas, S. & Chatterjee, S.K. 1985. Insecta: Coleoptera: Scarabaeidae: Coprinae. *Records of the Zoological Survey of India* 82: 147–177.

Blackburn, T. 1904. Revision of the Australian Aphodiides, and descriptions of three new species allied to them. *Proceedings of the Royal Society of Victoria, Melbourne* 17: 145–181.

Boheman, C.H. 1857. Insecta Caffrarie annis 1838–1845 a J.A. Wahlberg collecta amici auxilio suffultus descripsit. Coleoptera Officina Norstedtiana. *Holmiae* 2: 1–395. (Includes species described by Fåhraeus OJ. 1857).

Boheman, C.H. 1858. Coleoptera. In: Kongliga Svenska Fregatten Eugenies Resa Omkring Jorden under Befal af C.A.Virgin, Aren 1851–53. Vetenskapliga Iakttagelser Pa H.M.K.Oscar den Forstes. Kongliga svenska Vetenskapsakademien Handlingar, Stockholm, 40–58.

Boheman, C.H. 1860. Coleoptera Caffraria annis 1838-1845 a J.A. Wahlberg collecta. *Öfversigt Kongliga Svenska Vetenskapsakademiens Förhandlingar* 17: 107–120.

Bouchard, P., Bousquet, Y., Davies, A.E., Alonso-Zarazaga, M.A., Lawrence, J.F., Lyal, C.H.C., Newton, A.F., Reid, C.A.M., Schmitt, M., Slipinski, S.A. & Smith, A.B.T. 2011. Family-group names in Coleoptera. *Zookeys* 88: 1–972.

Boucomont, A. 1914. Les Coprophages de l'Archipel Malais. *Annales de la Société Entomologique de France, Paris* 83: 238–350.

Boucomont, A. 1920. Coprophaga Africana. Genre nouveau et espèces nouvelles. *Revue Zoologique Africaine, Bruxelles* 8: 261–269.

Boucomont, A. 1922. Les Coléoptères Coprophages du genre *Pedaria* Cast. *Bulletin du Musée Nationale d'Histoire naturelle, Paris* 28: 490–495.

Boucomont, A. 1923a. Scarabéides recueillis par le Marquis S. Patrizi dans l'Afrique Orientale Tropicale. *Annali del Museo Civico di Storia Naturale "Giacomo Doria", Genova (1923-1925)* 51: 86–100.

Boucomont, A. 1923b. Coprophaga africana, 2e note. *Revue Zoologique Africaine* 11: 40–58.

Boucomont, A. 1932. Coprophaga Africana 6e Note. *Revue de Zoologie africaine, Tervuren, Bruxelles* 22: 46–53.

Boucomont, A. 1936. Coprophaga Africana 8e Note. *Revue de Zoologie Africaine, Tervuren, Bruxelles* 28: 493–496.

Boucomont, A. & Gillet, J.J.E. 1927. Fam. Scarabaeidae. Subfam. Coprinae II. In Gillet, J.J.E. & Boucomont, *Scarabaeidae : Coprinae, Termitotroginae.* Coleopterorum Catalogus, auspiciis et auxilio W. Junk, editus a S. Schenkling. (Partes 38 et 90). W. Junk, Berlin 19: 103–263.

Branco, T. 1989. Étude de *Cambefortius* gen.n. et diagnose préliminaire de quatre nouveaux genres d'Onthophagini afrotropicaux (Coleoptera, Scarabaeidae). *Annales de la Société Entomologique de France* (*N.S.*) 25: 249–263.

Branco, T. 1991. Révision des genres du "groupe" *Stiptopodius*: les genres *Stiptopodius* et *Stiptotarsus*. *Annales de la Société Entomologique de France, Paris* (*N.S.*) 27: 265–285.

Branco, T. 2007. Scarabaeoidea (Coleoptera) of Portugal: genus-group names and their type species. *Zootaxa* 1453: 1–31.

Branco, T. 2010. Revision of the genera *Tiniocellus* Péringuey, 1901 and *Nitiocellus* gen. n. *Boletin de la Sociedad Entomologica Aragonesa* 47: 71–126.

Branco, T. 2011. Scarabaeidae de l'Afrique de l'Ouest : les noms du niveau genre et leurs espèces types. *Catharsius, La Revue* 4: 9–25.

Branco, T. & Josso, J.-F. 2007. Un nouveau *Pinacopodius* Branco, 1992 et un nouvel *Heteroclitopus* Péringuey, 1901, du Malawi. *Nouvelle Revue d'Entomologie* 24: 3–12.

Branco, T. & Ziani, S. 2005. *Cheironitis* Lansberge, 1875 - its correct spelling and validity. *Boletin de la Sociedad Entomologica Aragonesa* 37: 267–272.

Brauns, H. 1914. Descriptions of some new species of myrmecophilous beetles from southern Rhodesia, with a description of a new species of *Acritus* by Dr. H. Bickhardt (Cassel). *Proceedings of the Rhodesian Science Association* 13: 32–42.

Brown, J., Scholtz, C.H., Janeau, J.-L., Grellier, S. & Podwojewski, P. 2010. Dung beetles (Coleoptera: Scarabaeidae) can improve soil hydrological properties. *Applied Soil Ecology* 46: 9–16.

Burmeister, H. 1846. III. Coleoptera. 7. Lamellicornia. 27. *Copris*, 4 unnumbered pages. In: Genera Quaedam Insectorum. H. Burmeister (ed.). Privately published, Berlin, Germany.

Burmeister, H. 1873. Lamellicornia Argentina. *Stettiner Entomologische Zeitung* 34: 403–417.

Cambefort, Y. 1972. Scarabaeinae récoltés en Mauretanie par J.-L.Amiet. *Nouvelle Revue d'Entomologie, Paris* 2: 243–251.

Cambefort, Y. 1975. *Janssensellus,* un nouveau genre d'Onitini. *Bulletin de la Societe Entomologique de France, Paris* 80: 201–205.

Cambefort, Y. 1978. Canthonina nouveaux ou peu connus d'Afrique continentale. *Journal of the Entomological Society of Southern Africa* 41: 199–213.

Cambefort, Y. 1979. Données préliminaires sur la taxonomie des *Caccobius*. *Nouvelle Revue d'Entomologie, Paris* 9: 119–128.

Cambefort, Y. 1980. Nouveaux Onthophagides du Kenya. *Zoologische Mededelingen Leyden* 55: 195–200.

Cambefort, Y. 1981. La nidification du genre *Cyptochirus* (Coleoptera, Scarabaeidae). *Comptes Rendus de l'Academie des Sciences, Paris* 292: 379–381.

Cambefort, Y. 1982. *Pedaria* nouveaux ou peu connus de Cote d'Ivoire. *Revue française d'Entomologie* (*N.S.*) 4: 57–62.

Cambefort, Y. 1983. Nouveaux Scarabaeidae *s.str.* de Côte d'Ivoire et de pays voisins. *Revue française d'Entomologie* (*N.S.*) *Paris* 5: 7–9.

Cambefort, Y. 1984. Étude écologique des Coléoptères Scarabaeidae de Côte d'Ivoire. Annexe : Descriptions préliminaires d'un nouveau genre et de 36 nouvelles espèces, et nouvelle synonymie. *Travaux des chercheurs de la Station de Lamto (RCI)* 3: 1–12.

Cambefort, Y. 1985a. Révision du genre *Xinidium* Harold. *Annales de la Société Entomologique de France* 21: 95–102.

Cambefort, Y. 1985b. Les espèces orientales du genre *Cleptocaccobius*. *Revue française d'Entomologie* (*N.S.*) 7: 125–130.

Cambefort, Y. 1991b. Biogeography and evolution. In: Dung beetle ecology; Hanski I, Cambefort Y. (eds); Princeton University Press. Princeton, USA, 51–68.

Cambefort, Y. 1992a. Révision des espèces afrotropicales du genre *Copris* Müller, 1764. X. Espèces nouvelles ou peu connues. *Revue française d'Entomologie* (*N.S.*) 14: 179–183.

Cambefort, Y. 1992b. Revision des especes Afro-tropicales du genre *Copris* Müller, 1764 IX. Le groupe *urus* Boheman (Coleoptera, Scarabaeidae). *Bulletin de la Societe Entomologique de France* 97: 25–31.

Cambefort, Y. 1993. Notes brèves. Une nouvelle espèce du genre *Xinidium* Harold. *Annales de la Société Entomologique de France* 29: 103–105.

Cambefort, Y. 1996a. Une nouvelle espèce Afro-Tropicale d'*Euoniticellus* Janssens, 1953, avec une Phylogénie du genre. *Revue française d'Entomologie* (*N.S.*) *Paris* 18: 115–119.

Cambefort, Y. 1996b. Phylogénie et biogéographie du genre *Milichus* Péringuey, avec la déscription de cinq espèces et d›une sous-espèce nouvelles. *Bulletin de la Société Entomologique de France* 101: 159–169.

Cambefort, Y., Gill, B.D. & Moretto, P. 2010. Une nouvelle espèce du genre *Acanthonitis* Janssens. Contribution à la connaissance des genres d'Onitini. *Catharsius, La Revue* 2: 1–10

Cambefort, Y. & Mauchamp, B. 1980. Coléoptères Scarabaeinae nouveaux ou peu connus du Malawi. *Revue française d'Entomologie* (*N.S.*) 2: 177–181.

Castelnau, F.L. de. 1832. Mémoire sur cinquante espèces nouvelles ou peu connues d'insectes. *Annales de la Société Entomologique de France* 1: 386–415.

Castelnau, F.L. de. 1840. Histoire Naturelle des Insectes Coléoptères. Avec une introduction renfermant L'Anatomie et la Physiologie des Animaux Articulés, par M. Brullé. P. Duménil, Paris 2: 1–564.

Caveney, S., Scholtz, C.H. & McIntyre, P. 1989. Patterns of daily flight activity in onitine dung beetles (Scarabaeinae: Onitini). *Oecologia* 104: 444–452.

Chevrolat, A. 1830. In: Guérin-Méneville, F.E. 1844. Iconographie du Règne Animal de G.Cuvier. Part 7. Insectes. Ballière, Paris (1829-1844) 7: 1–576.

Costa, A. 1853. Coleotteri, Parte 1a. Famiglia degli Scarabeidei-Scarabaeidea. Costa O.G.:Fauna del Regno di Napoli ossie enumarazione di tutti gli animali che abitano le diverse regioni di questo Regno e le acque che le bagnano contenente la descrizione de' nuovi o poco esattemente conosciuti con figure ricavate da original viventi e dipinte al naturale. *G. Sautto, Napoli*, 1–44.

Creutzer, C. 1799. Entomologische Versuche (Kleine Beitrage zur nahren Berichtigungen einiger Kaferarten mit 3 ausgemahften Kupfertafeln von Sturm J.). Wien, Austria.

Daniel, G.M. 2019. The nomenclatural status of the generic nomina *Epirinus* Dejean, 1833 and *Epirhinus* Agassiz, 1846 (Coleoptera, Scarabaeidae, Scarabaeinae). *Bionomina* 15: 63–65.

Daniel, G.M., Davis, A.L.V. & Scholtz, C.H. 2016. Three new *Sisyphus* species from shaded vegetation in southern Africa. *Zootaxa* 4147: 67–74.

Daniel, G.M., Davis, A.L.V., Sole, C.L. & Scholtz, C.H. 2018. Taxonomic review of the tribe Sisyphini *sensu stricto* Mulsant, 1842 (Coleoptera: Scarabaeidae: Scarabaeinae) in southern Africa, including new species descriptions. *Insect Systematics & Evolution* 9: 1–61.

Daniel, G.M., Sole, C.L., Davis, A.L.V., Strümpher, W.P. & Scholtz, C.H. 2020. Systematics of the dung beetle tribe Sisyphini Mulsant (Scarabaeidae: Scarabaeinae) inferred from a molecular phylogeny and biogeography of southern African species. *Systematic Entomology* 45: 73–84.

Davis, A.L.V. 1986. Three new Afrotropical dung beetles in the genera *Kheper* Janssens, *Gymnopleurus* Illiger and *Onitis* Fabricius, with notes on related species. *Journal of the Entomological Society of Southern Africa* 49: 373–387.

Davis, A.L.V. 1993. Biogeographical groups in a southern African, winter rainfall, dung beetle assemblage (Coleoptera: Scarabaeidae) - consequences of climatic history and habitat fragmentation. *African Journal of Ecology* 31: 306–327.

Davis, A.L.V. 1994. Associations of Afrotropical Coleoptera (Scarabaeidae, Aphodiidae, Staphylinidae, Hydrophilidae, Histeridae) with dung and decaying matter: implications for selection of fly-control agents for Australia. *Journal of Natural History* 28: 383–399.

Davis, A.L.V. 1995. Daily weather variation and temporal dynamics in an Afrotropical dung beetle community (Coleoptera: Scarabaeidae). *Acta Oecologica* 16: 641–656.

Davis, A.L.V. 1996a. Diel and seasonal community dynamics in an assemblage of coprophagous, Afrotropical, dung beetles (Coleoptera: Scarabaeidae *s. str.*, Aphodiidae, Staphylinidae: Oxytelinae). *Journal of African Zoology* 110: 291–308.

Davis, A.L.V. 1996b. Habitat associations in a South African, summer rainfall, dung beetle community (Coleoptera: Scarabaeidae, Aphodiidae, Staphylinidae, Histeridae, Hydrophilidae). *Pedobiologia* 40: 260–280.

Davis, A.L.V. 1997. Climatic and biogeographical associations of southern African dung beetles (Coleoptera: Scarabaeidae *s. str.*). *African Journal of Ecology* 35: 10–38.

Davis, A.L.V. 2002. Dung beetle diversity in South Africa: influential factors, conservation status, data inadequacies, and survey design. *African Entomology* 10: 53–65.

Davis, A.L.V. & Deschodt, C.M. 2018. Two new species of *Garreta* Janssens, 1940 (Coleoptera: Scarabaeidae: Scarabaeinae) from southern Africa. *Zootaxa* 4450: 242–248.

Davis, A.L.V., Deschodt, C.M. & Scholtz, C.H. 2019. Describing new tribes to resolve discrepancies between phylogeny and tribal classification in the subfamily Scarabaeinae (Coleoptera: Scarabaeidae). *Zootaxa* 4608: 131–144.

Davis, A.L.V., Frolov, A.V. & Scholtz, C.H. 2008. *The African dung beetle genera.* Protea Book House, Pretoria: 1–272.

Davis, A.L.V. & Scholtz, C.H. 2020. Dung beetle conservation biogeography in southern Africa: current challenges and potential effects of climatic change. *Biodiversity and Conservation* 29: 667–693.

Davis, A.L.V., Scholtz, C.H. & Chown, S.L. 1999a. Species turnover, community boundaries, and biogeographical composition of dung beetle assemblages across an altitudinal gradient in South Africa. *Journal of Biogeography* 26: 1039–1055.

Davis, A.L.V., Scholtz, C.H. & Deschodt, C. 2005. A dung beetle survey of selected Gauteng nature reserves: implications for conservation of the provincial scarabaeine fauna. *African Entomology* 13: 1–16.

Davis, A.L.V., Scholtz, C.H., Dooley, P.W., Bham, N. & Kryger, U. 2004. Scarabaeine dung beetles as indicators of biodiversity, habitat transformation and pest control chemicals in agro-ecosystems. *South African Journal of Science* 100: 415–424.

Davis, A.L.V., Scholtz, C.H. & Harrison, J. du G. 1999b. New and threatened Afrotropical dung beetle taxa in the Gondwanaland tribe Canthonini. *African Entomology* 7: 77–84.

Davis, A.L.V., Scholtz, C.H. & Sole, C.L. 2017. Biogeographical and co-evolutionary origins of scarabaeine dung beetles: Mesozoic vicariance *versus* Cenozoic dispersal and dinosaur *versus* mammal dung. *Biological Journal of the Linnean Society* 120: 258–273.

Davis, A.L.V., Scholtz, C.H. & Swemmer, A.M. 2012. Effects of land usage on dung beetle assemblage structure: Kruger National Park versus adjacent farmland in South Africa. *Journal of Insect Conservation* 16: 399–411.

Davis, A.L.V., Stals, R. & Deschodt, C.M. 2015. New replacement name for the species *Scarabaeus* (*Scarabaeolus*) *nitidus* Davis & Deschodt, 2015 – not an American pest. *Zootaxa* 4057: 582.

Davis, A.L.V., Swemmer, A.M., Scholtz, C.H., Deschodt, C.M. & Tshikae, B.P. 2014. Roles of environmental variables and land usage as drivers of dung beetle assemblage structure in mopane woodland. *Austral Ecology* 39: 313–327.

Davis, A.L.V., Van Aarde, R.J., Scholtz, C.H. & Delport, J.H. 2002. Increasing representation of localized dung beetles across a chronosequence of regenerating vegetation and natural dune forest in South Africa. *Global Ecology and Biogeography* 11: 191–210.

Davis, A.L.V., Van Aarde, R.J., Scholtz, C.H., Guldemond, R.A.R., Fourie, J. & Deschodt, C.M. 2013. Is microclimate-driven turnover of dung beetle assemblage structure in regenerating coastal vegetation a precursor to re-establishment of a forest fauna? *Journal of Insect Conservation* 17: 565–576.

DeGeer, C. 1778. Mémoires pour servir à l'Histoire des Insectes (tom. 1-7. 1752-1778). Hesselberg, Stockholm 7: 1–950.

Dejean, P.F.M.A. 1821. Catalogue de la collection de Coléoptères de M. le Baron Dejean. Crevot Libraire, Paris: 136.

Dejean, P.F.M.A. 1833. Catalogue des Coléoptères de la collection de M. le Comte Dejean (1833-1835). Deuxième Édition. Méquignon-Marvis Père et Fils, Paris: 1–443.

Dejean, P.F.M.A. 1836. Catalogue des Coléoptères de la Collection de M. le Comte Dejean. Troisième Édition, Revue, Corrigée et Augmentée, Fascicles 1–4. Méquignon-Marvis Père et Fils, Paris, France.

Deschodt, C.M. & Davis, A.L.V. 2017. Transfer of three species of *Namakwanus* Scholtz & Howden to *Versicorpus* Deschodt, Davis & Scholtz or to *Namaphilus gen. nov.*, with descriptions of two new species (Coleoptera: Scarabaeidae: Scarabaeinae). *Annals of the Ditsong National Museum of Natural History* 7: 109–114.

Deschodt, C.M. & Davis, A.L.V. 2018. New deltochiline (Coleoptera: Scarabaeidae: Scarabaeinae) taxa associated with hyrax dung in arid south western Namibia. *Zootaxa* 4450: 066–076.

Deschodt, C.M. & Davis, A.L.V. 2019. New southern African species and a revalidation in the dung beetle genus *Gyronotus* van Lansberge, 1874 (Scarabaeidae: Scarabaeinae) with an updated key. *Zootaxa* 4624: 275–282.

Deschodt, C.M., Davis, A.L.V. & Daniel, G.M. 2019. The endemic southern African genus *Epirinus* Dejean, 1833 (Coleoptera: Scarabaeidae: Scarabaeinae) revisited: five new species and two new synonyms. *Zootaxa* 4603: 327–340.

Deschodt, C.M., Davis, A.L.V. & Scholtz, C.H. 2011. New dung beetle taxa from arid south-western Africa. *Insect Systematics & Evolution* 42: 277–294.

Deschodt, C.M., Davis, A.L.V. & Scholtz, C.H. 2015a. A new synonymy in the *fidius* group of *Copris* Müller 1764 and a new species from the highland grasslands of South Africa. *Zootaxa* 3949: 431–438.

Deschodt, C.M., Davis, A.L.V. & Scholtz, C.H. 2015b. Status changes, new synonymies, key and descriptions of seven new species in the subgenus *Scarabaeus* (*Scarabaeolus*) Balthasar 1965. *Zootaxa* 3931: 505–527.

Deschodt, C.M., Davis, A.L.V. & Scholtz, C.H. 2016. A new monotypic genus, a species synonymy and nomenclatural corrections in the arid-adapted Canthonini from the Succulent Karoo Biome of south-western Africa. *Zootaxa* 4147: 490–500.

Deschodt, C.M., Davis, A.L.V. & Scholtz, C.H. 2017. Three new species, a synonymy and taxonomic notes on southern African members of the dung beetle genera *Scarabaeus s. str.* Linnaeus, 1758 and *Escarabaeus* Zídek & Pokorný, 2011. *Journal of Natural History* 51: 299–316.

Deschodt, C.M., Davis, A.L.V. & Sole, C.L. 2019. A beautiful new species of *Hyalonthophagus* Palestrini & Giacone, 1988 (Coleoptera: Scarabaeidae: Scarabaeinae), from the Northern Cape Province, South Africa. *Zootaxa* 4648: 194–200.

Deschodt, C.M., Kryger, U. & Scholtz, C.H. 2008. New taxa of relictual Canthonini dung beetles utilizing rock hyrax middens as refuges in South-western Africa. *Insect Systematics & Evolution* 38: 361–376.

Deschodt, C.M. & Scholtz, C.H. 2008. Systematics of South African forest-endemic dung beetles: new genera and species of small Canthonini. *African Entomology* 16: 91–106.

Deschodt, C.M. & Sole, C.L. 2019. A new species of *Versicorpus* Deschodt, Davis & Scholtz, 2011 (Scarabaeidae: Scarabaeinae: Byrrhidiini) from the Brandberg Mountain, Namibia. *Zootaxa* 4671: 139–144.

Dormont, L., Jay-Robert, P., Bessière, J.-M., Rapior, S. & Lumaret, J.-P. 2010. Innate olfactory preferences in dung beetles. *Journal of Experimental Biology* 213: 3177–3186.

Doube, B.M. 1983. The habitat preference of some bovine dung beetles (Coleoptera: Scarabaeidae) in Hluhluwe Game Reserve, South Africa. *Bulletin of Entomological Research* 73: 357–371.

Doube, B.M. 1991. Dung beetles of southern Africa. In: Dung beetle ecology; Hanski I, Cambefort Y. (eds); Princeton University Press, Princeton, USA, 133–155.

Doube, B.M.1991. Appendix B.8. In: Dung beetle ecology; Hanski I, Cambefort Y. (eds); Princeton University Press, Princeton, USA, 382–387.

Doube, B.M., Giller, P.S. & Moola, F. 1988. Dung burial strategies in some South African coprine and onitine dung beetles. *Ecological Entomology* 13: 251–261.

Endrödi, S. 1971. The scientific Results of the Hungarian Zoological Expeditions to Tanganyika. 16. Coleoptera Lamellicornia (partim). *Folia Entomologica Hungarica, Budapest* 24: 289–311.

Endrödi, S. 1973. Entomological Explorations in Ghana by Dr. S. Endrody-Younga 14, Lamellicornia I. *Annales historico-naturales Musei nationalis hungarici, Budapest* 65: 195–229.

Endrödi, S. 1976. Lamellicornia aus Ghana II. *Annales historico-naturales Musei nationalis hungarici, Budapest* 68: 155–164.

Edwards, P.B. 1988. Field ecology of a brood-caring dung beetle *Kheper nigroaeneus* - habitat predictability and life history strategy. *Oecologia* 75: 527–534.

Edwards, P.B., & Aschenborn, H. 1987. Patterns of nesting and dung burial in *Onitis* dung beetles: implications for pasture productivity and fly control. *Journal of Applied Ecology* 24: 837–851.

Erichson, W.F. 1835. Neue Südamerikanische Käfergattungen aus der Familie der Blätterhörner. *Archiv für Naturgeschichte* 1: 256–270.

Erichson, W.F. 1843. Beitrag zur Insecten-Fauna von Angola, in besonderer Beziiehung zur geographischen Verbreitung der Insecten in Africa. *Archiv für Naturgeschichte, Berlin* 9: 199–267.

Erichson, W.F. 1847a. Conspectus Insectorum Coleopterum, quae in Republica Peruana observata sunt. *Archiv für Naturgeschichte* 13: 67–185.

Erichson, W.F. 1847b. Naturgeschichte der Insecten Deutschland. Erste Abteilung.Coleoptera. Dritter Band. Nicolaische Verlags-Buchhandlung, Berlin. Lieferung 5: 641–800.

Erichson, W.F. 1848. Naturgeschichte des Insecten Deutschland. I.Coleoptera, Scaphidilia, Scarabaeides. *Nicolaischen Buchhandlung, Berlin* (1847–1848) 1: 1–968.

Eschscholtz, J.F. 1822. Entomographien. O. Reimer, Berlin.

Excoffier, L., Laval, G. & Schneider, S. 2006. Arlequin ver. 3.1. An integrated software package for population genetics data analysis. Available at: <http://cmpg.unibe.ch/software/arlequin3> (Minimum Spanning Tree module no longer available as part of the Arlequin package).

Fabricius, J.C. 1775. Systema Entomologiae: sistens insectorum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus. *Officina Libraria Kortii. Flensburgi & Lipsiae*, 1–832.

Fabricius, J.C. 1776. Genera Insectorum corumque characteres naturales secundum numerum, figuram, situm et propotionem omnium partium oris, adiecta mantissa specierum. *Kiliae*: 1–310.

Fabricius, J.C. 1781. Species insectorum, exhibentes eorum differentias specificas, synonyma auctorum, loca natalia, metamorphosin, adiectis observationibus, descriptionibus. Tome I. Carol.Ernest.Bohnii, Hamburgi et Kilonii, VIII: 1–552.

Fabricius, J.C. 1792. Entomologia systematica emendata et aucta. Secundum Classes, Ordines, Genera, Species adjectis Synonimis, Locis, Observationibus, Descriptionibus. Hafniae 1: 1–538, C. G. Proft & fils.

Fabricius, J.C. 1794. Entomologia systematica emendata et aucta. Secundum Classes, Ordines, Genera, Species adjectis synonymis, locis, observationibus, descriptionibus. *Hafniae* 4: 1–472, CG Proft & fils.

Fabricius. J,C. 1798. Supplementum Entomologiae Systematicae. Hafniae: 1–572.

Fabricius, J.C. 1801. Systema Eleutheratorum secundum ordines, genera, species: adiectis synonymis, locis, observationibus, descriptionibus. Tomus I. Impensis bibliopoli academici novi, Kiliae: 1–506.

Fåhraeus, O.J. 1857. See Boheman, C.H. 1857.

Fairmaire, L. 1884a. Diagnoses des Coléoptères de l'Afrique orientale (suite). *Annales de la Société Entomologique de Belgique. Comptes Rendus des seances, Bruxelles* 28: 121–125.

Fairmaire, L. 1884b. Diagnoses des Coléoptères de l'Afrique. *Annales de la Société Entomologique de Belgique. Comptes Rendus des seances Bruxelles* 28: 142–149.

Fairmaire, L. 1887. Coléoptères des voyages de M.G.Revoil chez les Somalis et dans l'interieur du Zanguebar. *Annales de la Société Entomologique de France, Bulletin* 7: 102–134.

Fairmaire, L. 1888. Enumération des Coléoptères recueillis par M. le Dr.Hans Schinz dans le Sud de l'Afrique. *Annales de la Société Entomologique de France, Paris* 6: 173–202.

Fairmaire, L. 1891. Coléoptères de l'Afrique Orientale. *Annales de la Société Entomologique de Belgique. Compte Rendus des Séances* 35: 279–289.

Fairmaire, L. 1893. Note sur les Coléoptères de Choa. *Annales de la Société Entomologique de Belgique. Compte Rendus des Séances* 37: 9–50.

Felsche, C. 1907. Coprophage Scarabaeiden. *Deutsche Entomologische Zeitschrift*, 273–296.

Felsche, C. 1909. Neue und alte coprophage Scarabaeiden. *Deutsche Entomologische Zeitschrift*, 751–765.

Felsche, C. 1911. Coprophage Scarabaeiden. *Deutsche Entomologische Zeitschrift*, 133–141.

Ferreira, M.C. 1952a. Duas espécies novas de *Scarabaeus* da África do Sul. *Boletim Sociedade de Estudos da Provincia de Moçambique* 22: 19–24.

Ferreira, M.C. 1952b. A new species of *Scarabaeus*. *Annals of the Transvaal Museum, Pretoria* 22: 73–77.

Ferreira, M.C. 1953a. Monografia dos Escarabaeideos da Africa do Sul. Tribo-Scarabaeini. I Parte Sub-tribo Pachysomides. *Boletim Sociedade de Estudos da Provincia de Moçambique* 23: 1–80.

Ferreira, M.C. 1953b. Contribuiçao para o estudo dos Escarabaeídeos da Africa do Sul. Aditamento à I parte da Monografia dos Escarabaeideos da Africa do Sul. *Boletim Sociedade de Estudos da Provincia de Moçambique* 80: 1–9.

Ferreira, M.C. 1953c. Contribuiçao para o estudo dos Escarabaeídeos da África do Sul. *Memorias Museum Dr. Alvaro de Castro. Lourenço Marques* 2: 23–26.

Ferreira, M.C. 1954a. Monografia dos Escarabaeídeos da África do Sul. V. Parte. *Boletim Sociedade de Estudos da Provincia de Moçambique* 87: 1–15.

Ferreira, M.C. 1954b. Contribuiçao para o estudo dos Escarabídeos da África do Sul. Uma nova espécie do género *Gymnopleurus* Illiger. *Boletim Sociedade de Estudos da Provincia de Mocambique* 84: 1–4.

Ferreira, M.C. 1954c. Algumas variedades novas de Gymnopleurineos e notas sinonimicas. *Boletim Sociedade de Estudos da Provincia de Mocambique* 85: 1–3.

Ferreira, M.C. 1954d. Some Scarabaeina in the Durban Museum and Art Gallery. *Durban Museum Novitates, Durban* 4: 91–95.

Ferreira, M.C. 1958a. Duas espécies novas do género *Copris* Geoff. *Novos Taxa Entomológicos* 9: 3–5.

Ferreira, M.C. 1958b. Coleoptera Scarabaeidae. Coprinae. Results of the Lund University Expedition in 1950-1951. In: B. Hanström, P. Brinck, G. Rudebeck eds. *South African Animal Life* 5: 479–516.

Ferreira, M.C. 1958b. A new species of *Scarabaeus* from Angola. *Novos Taxa Entomológicos* 1: 3–6.

Ferreira, M.C. 1958c. A new species of *Scarabaeus* from South West Africa. *Novos Taxa Entomológicos* 5: 3–4.

Ferreira, M.C. 1960a. Revisao das espécies africanas de *Catharsius s.str*. Do grupo adamastor e descricao de especies novas. *Revista Entomologia Moçambique* 3: 1–77.

Ferreira, M.C. 1960b. Revisao das espécies etiopicas do subgenero *Catharsius s.str. Revista Entomologia Moçambique* 3: 155–270.

Ferreira, M.C. 1962a. Contribuçao para o conhecimento dos Escarabídeos de Angola. *Publiçoes cultural Companhia Diamantes Angola* 54: 121–190.

Ferreira, M.C. 1962b. Exploration du Parc National de la Garamba. Coprinae. Institut des Parcs Nationaux du Congo et du Rwanda. Mission H. De Saeger (1949–1952). Fascicule 30: 1–123.

Ferreira, M.C. 1963. Contribuiçao para o conhecimento dos Escarabídeos africanos. *Novos Taxa Entomológicos* 30: 3–39.

Ferreira, M.C. 1964a. Contribuiçao para o estudo do género *Epirinus* Reiche. *Novos Taxa Entomológicos* 37: 3–13.

Ferreira, M.C. 1964b. Contribuiçao para o estudo do subgénero *Metacatharsius* Paulian. Descriçao de especies novas. *Novos Taxa Entomológicos* 34: 3–32.

Ferreira, M.C. 1965. Contribuiçao para o estudo dos Escarabídeos de Moçambique. Descriçao de uma espécie nova do subgénero *Metacatharsius* Paulian. *Novos Taxa Entomológicos* 45: 3–10.

Ferreira, M.C. 1968. Contribuiçao para o estudo dos Escarabídeos de Moçambique. Descriçao de uma espécie nova do subgénero *Scarabaeolus* Balthasar. *Novos Taxa Entomológicos* 58: 3–9.

Ferreira, M.C. 1969. Contribuiçao para o conhecimento dos Escarabídeos de África. Descriçao de uma espécie nova de *Scarabaeus s. str. Novos Taxa Entomológicos* 68: 3–4.

Ferreira, M.C. 1971. Contribuiçao para o estudo dos Escarabídeos Africanos. Descriçao de uma espècie nova de *Catharsius s.str. Novos Taxa Entomológicos* 96: 5–6.

Ferreira, M.C. 1972 (1968–1972). Os escarabídeos de África (sul do Sáara). *Revista Entomologia Moçambique* 11: 1–1088.

Ferreira, M.C. 1976a. A. Some new species of *Onitis* F. (Coleoptera: Scarabaeidae). B. A new species of *Chironitis* Lansberge (Coleoptera : Scarabaeidae). *Navorsinge van die Nasionale Museum* 3 (9): 181–198.

Ferreira, M.C. 1976b. A new species of *Platyonitis* Janssens from Angola. *Navorsinge van die Nasionale Museum* 3 (8): 177–180.

Ferreira, M.C. 1977. Contribution to the knowledge of the African Scarabaeidae. A new genus of Onitini and some new species of *Onitis* F. *Navorsinge van die Nasionale Museum* 3 (10): 181–198.

Ferreira, M.C. 1978. The genus *Onitis* F. of Africa south of the Sahara. *Memoirs van die Nasionale Museum* 10: 1–410.

Fincher, G.T. 1973. Nidification and reproduction of *Phanaeus* spp. in three textural classes of soil (Coleoptera: Scarabaeidae). *Coleopterists Bulletin* 27: 33–37.

Forgie, S.A., Grebennikov, V.V. & Scholtz, C.H. 2002. Revision of *Sceliages*, a millipede-eating genus of southern African dung beetles. *Invertebrate Systematics* 16: 931–955.

Forgie, S.A., Philips, T.K. & Scholtz, C.H. 2005. Evolution of the Scarabaeini (Scarabaeidae: Scarabaeinae). *Systematic Entomology* 30: 60–96.

Forgie, S.A., Kryger, U., Bloomer, P. & Scholtz, C.H. 2006. Evolutionary relationships among the Scarabaeini (Coleoptera: scarabaeidae) based on combined molecular and morphological data. *Molecular and Phylogenetic Evolution* 40: 662–678.

Frey, G. 1955. Coprophagen-Studien über neue und wenig bekannte Arten. *Entomologische Arbeiten aus dem Museum G. Frey* 6: 1057–1066.

Frey, G. 1963. Neue Onthophagen aus Australien und aus Afrika. *Entomologische Arbeiten aus dem Museum G. Frey* 14: 538–549.

Frey, G. 1967. Zwei neue afrikanische Coprophagen sowie eine neue Synonymie. *Entomologische Arbeiten aus dem Museum G. Frey* 18: 404–405.

Frey, G. 1975a. Neue Coprophagen aus dem Zentralafrikanischen Museum in Tervuren und aus meine museum. *Entomologische Arbeiten aus dem Museum G.Frey* 26: 292–296.

Frey, G. 1975b. Neue Sudafrikanische Onthophagini gesammelt vom dung beetle research unit Pretoria. *Entomologische Arbeiten aus dem Museum G. Frey* 26: 191–197.

Frolov, A.V. 2004. New and little known species of the Afrotropical dung beetle genus *Sarophorus* and a phylogenetic analysis of the genus. *Journal of Afrotropical Zoology* 1: 95–100.

Frolov, A.V. 2014. Revision of the genus *Delopleurus* Boheman (Coleoptera: Scarabaeidae: Scarabaeinae) with description of new species from Africa. *Journal of Natural History* 49: 129–154.

Frolov, A.V., Akhmetova L.A. & Scholtz, C.H. 2008. Revision of the obligate mushroom-feeding African "dung beetle" genus *Coptorhina* Hope (Coleoptera: Scarabaeidae: Scarabaeinae). *Journal of Natural History* 42: 1477–1508.

Frolov, A.V. & Scholtz, C.H. 2003a. Revision of the Afrotropical dung beetle genus *Sarophorus* Erichson. *African Entomology* 11: 183–198.

Frolov, A.V. & Scholtz, C.H. 2003b. A new genus and species of dung beetle from southern Namibia. *African Entomology* 11: 297–299.

Frolov, A.V. & Scholtz, C.H. 2004. Revision of the southern African genus *Macroderes* Westwood. *Annales de la Société Entomologique de France* (*N.S.*) 40: 373–393.

Frolov, A.V. & Scholtz, C.H. 2005. Revision of the southern African genus *Frankenbergerius* Balthasar with description of new taxa. *Journal of Natural History* 39: 2355–2377.

Füessly, J.C. 1775. Verzeichnis der ihm bekannten Schweizerischen Insecten mit einer ausgemahlten Kupfertafel, nebst der Unkundigung eines neuen Insekten Werks. Winterthur & Füessly, Zürich: 1–62.

Gebler, F.A. 1841. Characteristik mehrerer neuen Sibirischen Coleopteren. *Bulletin scientific publié par Académie impériale des Sciences de Saint-Petersbourg* 8: 369–376.

Génier, F. 2013. Transfert d'*Onthophagus bubalus* Harold, 1867, dans le genre *Phalops* Erichson, 1847, et notes sur sa position phylogénétique. *Catharsius, La Revue* 7: 1–4.

Génier, F. & Moretto, P. 2017. *Digitonthophagus* Balthasar, 1959: taxonomy, systematics, and morphological phylogeny of the genus revealing an African species complex (Coleoptera: Scarabaeidae: Scarabaeinae). *Zootaxa* 4248: 1–110.

Génier, F. & Davis, A.L.V. 2017. *Digitonthophagus gazella auctorum*: an unfortunate case of mistaken identity for a widely introduced species (Coleoptera: Scarabaeidae: Scarabaeinae: Onthophagini). *Zootaxa* 4221: 497–500.

Génier, F. & Josso, J.-P. 2016. Notes on Afrotropical *Catharsius* species described by Edgar von Harold (Coleoptera: Scarabaeidae, Scarabaeinae). *Zootaxa* 4072: 333–342.

Geoffroy, E.L. 1762. *Histoire Abrégée des Insectes*, volume 1. Calixte-Volland and Rémont, Paris.

Gerstaecker, A. 1871. Beitrag zur Insektenfauna von Zanzibar. III. Coleoptera. *Archiv für Naturgeschichte, Berlin* 37: 42–349.

Gerstaecker, A. 1873. Die Gliedertier-Fauna des Sansibar-Gebietes. Decken C. C. Baron Carl Claus von der Decken's Reisen in Ost Afrikas, Berlin: 1–542.

Gerstaecker, A. 1884. Bestimmungen der von Herrn Dr. G.A. Fischer wahrend seiner Reise nach dem Massai-Land gesammelten Coleopteren. *Jahresbuch der hamburgischen Wissenschaftlichen Anstalten, Hamburg (1883)* 1: 43–63.

Gestro, R. 1895. Esplorazione del Giuba e dei suoi affluenti compiuta dal cap. V. Bottegno durante gli anii 1892-93 sotto gli auspici della società geografica italiana. Risultati zoologici. XVI. Coleotteri. *Annali del Museo civico di Storia Naturale di Genova, Genova* (*Series 2*) 15: 309–341.

Giller, P.S. & Doube, B.M. 1994. Spatial and temporal co-occurrence of competitors in Southern African dung beetle communities. *Journal of Animal Ecology* 63: 629–643.

Gillet, J.J.E. 1907. Remarques sur quelques coprides du Museo Civico de Gênes. *Annali del Museo Civico di Storia Naturale "Giacomo Doria", Genova* 3: 587–603.

Gillet, J.J.E. 1908. Coprides d'Afrique tropicale. Descriptions d'espèces nouvelles et remarques sur quelques espèces connues. *Mémoires de la Société Entomologique de Belgique* 16: 63–82.

Gillet, J.J.E. 1909. Collections receuillis dans le Sahara et régions voisines, par René Chudeau. *Bulletin du Muséum nationale d'Histoire Naturelle, Paris* 15: 432–437.

Gillet, J.J.E. 1911. Coprophaga Africana. Descriptions d'espèces nouvelles et remarques diverses. *Annales de la Société Entomologique de Belgique* 55: 308–312.

Gillet, J.J.E. 1918. Coprides nouveaux de la région éthiopienne et remarques diverses. *Zoologische Mededelingen, Leiden* 4: 146–158.

Gistel, J. 1857. Achthundert und zwanzig neue oder unbeschriebene wirbellose Thiere charakterisirt von Doctor Johannes Gistel. Schorner'sche Buchhandlung, Straubing. *Vacuna* 2: 513–606.

Goeze, J.A.E. 1777. Entomologische Beytrage zu des Ritter Linne zwolften Ausgabe des Natursystems. Weidmanns, Erben und Reich, Leipzig 1: 1–736.

Gomes Alves, M.-L. 1954. Alguns Escarabídeos de Moçambique – II. Junta das Missões Geográficas e de Investigações do Ultramar, Lisboa. Anais, Vol. IX, Tomo III. Estudos de Zoologia. *Trabalhos da Missão Zoológica de Moçambique e do Centro de Zoologia* (1957) 9: 55–61.

Gory, M. 1833. *Monographie du genre Sisyphe.* Mequignon-Marvis pere et fils, Paris: 1–15.

Griffith, E. & Pidgeon, E. 1831. The Class Insecta arranged by the Baron Cuvier, with Supplementary Additions to each Order. Notices of New Genera and Species by G. Gray. Volume the first. 446-537 In: *The Animal Kingdom arranged in conformity with its Organisation by the Baron Cuvier, with Supplementary Additions to each Order*; Griffith E. et al. (eds); Volume 14 (dated 1832). Whittaker, Treacher, & Co., London: 1–570.

Guérin-Méneville, F.E. 1844. Iconographie du Règne Animal de G. Cuvier. Part 7. Insectes. Ballière, Paris (1829–1844) 7: 1–576.

Haaf, E. 1955. Uber die gattung Sisyphus Latreille. *Entomologische Arbeiten aus dem Museum G. Frey* 6: 341–381.

Halffter, G. & Favila ME. 1993. The Scarabaeinae (Insecta: Coleoptera): an animal group for analyzing, inventorying and monitoring biodiversity in tropical rainforest and modified landscapes. *Biodiversity International* 27: 15–21.

Hanski, I. & Cambefort, Y. 1991a. Competition in dung beetles. In: *Dung beetle ecology*; Hanski I, Cambefort Y. (eds); Princeton University Press, Princeton: 305–329.

Hanski, I. & Cambefort, Y. 1991b. Index of the genera in Scarabaeidae. In: *Dung beetle ecology*; Hanski I, Cambefort Y. (eds); Princeton University Press, Princeton: 465–473.

Harold, E. von. 1859. Beitrage zur kenntnis einiger coprophagen lamellicornien. (I. Stück). *Berliner Entomologische Zeitschrift, Berlin* 3: 193–224.

Harold, E. von. 1862. Beiträge zur Kenntniss einiger coprophagen Lamellicornien (Viertes Stuck). *Berliner Entomologische Zeitschrift, Berlin* 6: 379–403.
Harold, E. von. 1867a. Zur Kenntniss der Gattung Canthidium und ihrer nächsten Verwandten. *Coleopterologische Hefte* 1: 1–61.
Harold, E. von. 1867b. Zur Synonymie zweier Gymnopleurus-Arten. *Coleopterologische Hefte* 1: 73–75.
Harold, E. von. 1867c. Beiträge zur Kenntniss der Gattung Onthophagus (I.Theil: Australier und Afrikaner). *Coleopterologische Hefte* 2: 23–59.
Harold, E. von. 1868a. Diagnosen neuer Coprophagen. *Coleopterologische Hefte* 4: 79–86.
Harold, E. von. 1868b. Abänderungen vergebener Namen. *Coleopterologische Hefte* 4: 104.
Harold, E. von. 1868c. Diagnosen neuer Coprophagen. *Coleopterologische Hefte* 3: 80–86.
Harold, E. von. 1869a. Diagnosen neuer Coprophagen. *Coleopterologische Hefte* 5: 95–104.
Harold, E. von. 1869b. Ueber coprophage Lamellicornien mit besonderer Berücksichtigungen der Pariser Sammlungen. *Coleopterologische Hefte* 5: 46–70.
Harold, E. von. 1870. Berichtigungen und Zusätze zum Catalogus Coleopterorum synonymicus et systematicus. *Coleopterologische Hefte* 6: 94–110.
Harold, E. von. 1871a. Diagnosen neuer Coprophagen. *Coleopterologische Hefte, Munchen* 7: 112.
Harold, E. von. 1871b. Verzeichniss der von Dr. Beccari in Bogos gesammelten coprophagen Lamellicornien. *Coleopterologische Hefte, Munchen* 8: 1–28.
Harold, E. von. 1871c. Diagnosen neuer Coprophagen. *Coleopterologische Hefte* 8: 114–116.
Harold, E. von. 1873. Diagnosen neuer coprophagen. *Coleopterologische Hefte* 11: 102–105.
Harold, E. von. 1875. Diagnosen neuer Arten. *Coleopterologische Hefte* 14: 137–140.
Harold, E. von. 1877a. Enumeration des Lamellicorn coprophages rapportes de l'Archipel Malais, de la Nouvelle Guinée et de l'Australie boreale par M.M.J. Doria, O. Beccari et L.M. D'Albertis. *Annali del Museo Civico di Storia Naturale di Genova* 10: 38–110.
Harold, E. von. 1877b. Coleopterorum species novae. *Mitteilungen der munchner entomologischen Verein, Munchen* 1: 97–111.
Harold, E. von. 1878. Ueber Coleopteren aus dem tropischen Afrika. *Mittheilungen der munchner entomologischen Verein, Munchen* 2: 38–48.
Harold, E. von. 1880. Einige neue Coleopteren. *Mitteilungen der munchner entomologischen Verein, Munchen* 4: 148–171.
Harold, E. von. 1886. Coprophage Lamellicornien beschrieben von E. von Harold. *Berliner Entomologische Zeitschrift, Berlin* 30: 141–149.
Harrison, J. du G., Scholtz, C.H. & Chown, S.L. 2003. A revision of the endemic south-western African dung beetle subgenus *Scarabaeus* (*Pachysoma*), including notes on other flightless Scarabaeini. *Journal of Natural History* 37: 305–355.
Hausmann, J.F.L. 1807. Beiträge zur Insektenfauna des Vorgebirges der guten Hoffnung. *Magazin für Insektenkunde, K. Illiger, Braunschweig* 6: 229–267.
Herbst, J.F.W. 1789. Der Käfer. Jablonsky C.G.: Natursystem aller bekannten in- und auslandischen Insecten, als eine Fortsetzung der von Büffonschen Naturgeschichte. Nach dem System des Ritters von Linné und Fabricius. Ben Joachim Pauli, Berlin 2: 1–330.
Hoffmannsegg, J.C. 1817. Entomologische Bemerkungen bei Gelegenheit der Abhandlungen über amerikanische Insecten. *Zoologisches Magazin* 1: 8–56.
Hope, F.W. 1833. Characters of several new genera and species of Coleopterous Insects. *Proceedings of the Zoological Society, London* 1: 61–64.
Hope, F.W. 1837. The Coleopterists Manual, Containing the Lamellicorn Insects of Linneus and Fabricius. Henry G. Bohn, London: 121.
Hope, F.W. 1838. Observations on the lamellicorns of Olivier. *The Entomological Magazine* 5: 312–326.
Hope, F.W. 1842. On some new insects from Western Africa. *The Annals and Magazine of natural History, including Zoology, Botany and Geology* 1: 494–496.
Houston, W.W.K. 1983. Identification of the dung beetles *Onitis crenatus* Reiche from Ethiopia and *O. crenatus sensu* Boheman from southern Africa. *Journal of the Entomological Society of Southern Africa* 46: 249–256.
Howden, H. & Scholtz, C.H. 1987. A revision of the African genus *Odontoloma*. *Journal of the Entomological Society of Southern Africa* 50: 155–192.
Howden, H. & Scholtz, C.H. 1988. A second species of the African genus *Peckolus*. *Journal of the Entomological Society of Southern Africa* 51: 133–136.
ICZN. 1993. Opinion 1708. *Proagoderus* Lansberge, 1883 (Insecta, Coleoptera) : conserved. *The Bulletin of Zoological Nomenclature* 50: 75–76.
Illiger, J.K.W. 1803. Verzeichniss der in Portugal einheimischen Käfer. Erste Lieferung. *Magazin für Insektenkunde* 2: 186–258.
Inouchi, J. & Shibuya, T. 1986. Odour responses of the olfactory receptor cells in the dung beetles. *Chemical Senses* 11: 286.
IUCN. 2001. IUCN Red List Categories and Criteria: Version 3.1. IUCN Species Survival Commission. IUCN, Gland, Switzerland and Cambridge, UK.
Jacobson, F.V.S. 1906. Revue critico-bibliographique. Kolbe. H.J. Ueber die Lebensweise und die geographische Verbreitung der coprophagen Lamellicornien. *Russkoe Entomologicheskoe Obozrenie* 6: 312–315.
Jacobs, C.T. & Scholtz, C.H. 2015. A review on the effect of macrocyclic lactones on dung-dwelling insects: Toxicity of macrocyclic lactones to dung beetles. *Onderstepoort Journal of Veterinary Research* 82: 8.
Jankielsohn, A., Scholtz, C.H. & Louw, S. v.d. M. 2001. Effect of habitat transformation on dung beetle assemblages: a comparison between a South African nature reserve and neighboring farms. *Environmental Entomology* 30: 474–483.
Janssens, A. 1936. Un nouveau genre d'Onitide africain. *Bulletin du Musée royal d'Histoire Naturelle de Belgique, Bruxelles* 12: 1–3.
Janssens, A. 1937. Révision des Onitides. *Verhandelingen Koninklijk Natuurhistorisch Museum Belgie, Brussel* 2: 1–200.
Janssens, A. 1938a. Exploration du Parc National Albert. Scarabaeini. *Institut des parcs nationaux du Congo Belge* 21: 1–76.
Janssens, A. 1938b. Notes sur les Onitides africains (Coleoptera Lamellicornia), Troisième Note. *Bulletin du Musée royal d'Histoire naturelle de Belgique* 14: 13.
Janssens, A. 1939a. Exploration du Parc National Albert. Mission G.F. De Witte (1933-1935). Coprini. *Institut des parcs nationaux du Congo Belge* 29: 1–104.

Janssens, A. 1939b. Contribution à l'étude des Coléoptères Lamellicornes Coprophages. *Bulletin du Musée Royal d'Histoire Naturelle de Belgique, Bruxelles* 15 :1–6.

Janssens, A. 1940a. Monographie des Gymnopleurides (Coleoptera Lamellicornia). *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, 2e sér. 18: 1–74.

Janssens, A. 1940b. Monographie des *Scarabaeus* et genres voisines. *Verhandelingen Koninklijk Natuurhistorisch Museum Belgie, Brussel* 2: 1–81.

Janssens, A. 1942. Contribution à l'étude des Coléoptères Lamellicornes Coprophages. V. Quelques Onitides nouveaux ou peu connus. *Bulletin du Musée royal d'Histoire Naturelle de Belgique, Bruxelles* 18:1–9.

Janssens, A. 1943. Contribution a l'étude des coléoptères Lamellicornes coprophages. VII. Notes sur quelques Coprinae d'Afrique. *Bulletin du Musée royal d'Histoire Naturelle de Belgique* 19: 1–8.

Janssens, A. 1946. Contribution à l'étude des coléoptères lamellicornes coprophages, XI. - Table synoptique et essai de classification pratique des Scarabaeidae Laparosticti. *Bulletin du Musée Royal d'Histoire Naturelle de Belgique* 22: 1–13.

Janssens, A. 1949. Un Scarabaeinae termitophile nouveau du Congo Belge. *Revue de Zoologie et de Botanique africains, Bruxelles* 42: 183–184.

Janssens, A. 1950. Contribution à l'étude des Coléoptères Lamellicornes. XV. Un nouveaux et curieux genre d'Onitini. *Bulletin de l'Institut royal des Sciences naturelle de Belgique, Bruxelles* 26: 1–4.

Janssens, A. 1953. Exploration du Parc National de l'Upemba. Mission G.F. De Witte (1946-1949). Oniticellini. *Institut des parcs nationaux du Congo Belge* 11: 1–118.

Josso, J.F. 2011. Description de quatre nouvelles espèces de Scarabaeidae de Zambie, appartenant aux genres *Catharsius* Hope, 1837, *Copris* Müller, 1764, *Pleuronitis* Lansberge, 1875 et *Onthophagus* Latreille, 1802. *Catharsius, La Revue* 3: 1–8.

Josso, J.F. 2012. Les *Onitis* Fabricius, 1798 du Groupe XI de Janssens : redéfinition du groupe, mise en synonymie, description de six espèces nouvelles et clé de détermination. *Catharsius, La Revue* 5: 6–15.

Josso, J.F. 2014. Description de quatre nouvelles espèces de *Proagoderus* Lansberge, 1883, de Zambie, du Mozambique et du Malawi. *Catharsius, La Revue* 10: 1–8.

Josso, J.F. & Prévost, P. 2001. Contribution à la connaissance des Scarabaeidae africains I. *Les Cahiers Magellanes Hors Série* 2: 1–14.

Josso, J.F. & Prévost, P. 2003. Contribution à la connaissance des Scarabaeidae africains II. Etude du genre *Pedaria*. *Les Cahiers Magellanes Hors Série* 7: 1–39.

Josso, J.F. & Prévost, P. 2006a. Contribution à la connaissance des Scarabaeidae africains III, étude du genre *Pedaria* (2). *Les Cahiers Magellanes Hors Série* 14: 1–20.

Josso, J.F. & Prévost, P. 2006b. Description de cinq Onthophagini nouveaux pour l'Afrique de l'Ouest (Parc du W). *Les Cahiers Magellanes Hors Série* 21: 1–10.

Josso, J.F. & Prévost, P. 2009a. Contribution à la connaissance des Scarabaeidae africains IV. Etude du genre *Pedaria* (3). *Les Cahiers Magellanes Hors Série* 30: 1–22.

Josso, J.F. & Prévost, P. 2009b. Description de trois nouvelles espèces de *Catharsius* de Zambie et Tanzanie. *Les Cahiers Magellanes Hors Série* 31: 1–8.

Kabakov, O.N. 2006. Beetles of the subfamily Scarabaeinae of the fauna of Russia and adjacent countries. Moscow, *Scientific publications KMK*: 1–374.

Kirby, W. 1818. A century of insects, including several new genera described from his cabinet. *Transactions of the Linnean Society, London* 12: 375–453.

Kirby, W. 1828. A description of some Coleopterous insects in the collection of the Rev. F.W. Hope. *Zoological Journal* 3: 520–525.

Klug, J.C.F. 1835. V. Insekten (Coleoptera). In: Verzeichniss von Thieren und Pflanzen, welche auf einer Reise um die Erde gesammelt wurden von A. Erman. G. Reimer, Berlin, 27–50.

Klug, J.C.F. 1855. Diagnosen der neuer Coleopteren aus Mossambique. *Berichten der Koniglich-Preussischen Akademie der Wissenschaften, Berlin* 20: 643–660.

Klug, J.C.F. 1862. Peters W.C.H.: Naturwissenschaftliche Reise nach Mossambique auf Befehl Seiner Majestät des Königs Friedrich Wilhelm IV in den Jahren 1842 bis 1848 ausgeführt. Zoologie V. Insecten und Myriapoden. Georg Reiner, Berlin: 1–566.

Kolbe, H.J. 1887. Beiträge zur Zoogeographie Westafrikas nebst einem Bericht über die während der Loango-Expedition von Herrn Dr. Falkenstein bei Chinchoxo gesammelten Coleoptera. *Nova Acta Caesareae Leopoldina Carolinae germanicae naturae curiosorum Halle* 50: 153–364.

Kolbe, H.J. 1893a. Ueber afrikanische Mistkäfer (*Catharsius*, *Diastellopalpus*). *Sitzungsbericht der Gesellschaft naturforschender Freunde zu Berlin*: 131–151.

Kolbe, H.J. 1893b. Beiträge zur Kenntniss der Mistkafer, Lamellicornia Onthophila. *Stettiner entomologische Zeitung, Stettin* 54: 188–202.

Kolbe, H.J. 1895. Beiträge zur Kenntniss der Mistkafer, Lamellicornia Onthophila. *Stettiner entomologische Zeitung, Stettin* 56: 329–345.

Kolbe, H.J. 1897. Käfer und Netzflüger Ost-Afrikas. Moebius K.: Deutsch Ostafrika. Wissenschaftliche Forschungsresultate über Land und Leute unseres ostafrikanischen Schutzgebietes und der Angrenzenden Länder. Band IV. Die Thierwelt Ost-Afrikas und der Nachbargebiete. Wirbellose Thiere, Coleopteren. Dietrich Reimer, Berlin 4: 1–367.

Kolbe, H.J. 1905. Über die Lebensweise und die geographische Verbreitung der coprophagen Lamellicornier. *Zoologische Jahrbücher, Supplement* 8: 475–594.

Kolbe, H.J. 1908. Dynastidae, Cetoniidae und Scarabaeidae. Schultze L.: Zoologische und Arthropologische ergebnisse einer forschungsreise im westlichen und zentralen südafrika. Bd.1. *Denkschrift Medizinisch-Naturwissenschaftlichen Gesellschaft zu Jena* 13: 121–132.

Kolbe, H.J. 1914. Wissenschaftliche Ergebnisse der deutschen Zentral-Afrika-Expedition 1907-1908 unter Führung Adolf Friedrichs, Herzog zu Mecklemburg. Band V: Zoologie III. Lieferung 3. Scarabaeiden. Klinkhardt & Biermann, Leipzig 5: 261–416.

Kraatz, G. 1895. Zwei neue westafrikanische *Oniticellus*. *Deutsche Entomologische Zeitschrift, Berlin* 34: 142–144.

Krajcik, M. 2006. New species of *Kheper* Janssens from Namibia. *Animma* X 14: 19–23.

Král, D. 2014. *Delopleurus mencli* sp. nov. from Socotra Island. *Acta Entomologica Musei Nationalis Pragae* 54 (supplementum), 133–138.

Kràl, D. & Rejsek, J. 1999. The *Liatongus* species with moveable clypeal horn. *Folia Heyrovskyana Supplementum* 5: 1–18.

Krell, F.-T. 2004. East African dung beetles (Scarabaeidae) attracted by defensive secretions of millipedes. *Journal of East African Natural History* 93: 69–73.

Krell, F.-T., Branco, T. & Ziani, S. 2012. Case 3590 Scarabaeus Linnaeus, 1758, Dynastes MacLeay, 1819, SCARABAEINAE Latreille, 1802, and DYNASTINAE MacLeay, 1819 (Insecta, Coleoptera, SCARABAEOIDEA): proposed conservation of usage. *Bulletin of Zoological Nomenclature* 69: 182–190.

Krell, F.-T. & Philips, K. 2010. *Formicdubius* Philips & Scholtz from South Africa, a junior synonym of *Haroldius* Boucomont, and a survey of the trichomes in the African species. *Zookeys* 34: 41–48.

Krikken, J. 1974. A new species of *Platyonitis* Janssens from Kenya, with notes on the genus. *Zoologische Mededelingen Leyden* 48: 195–203.

Krikken, J. 1977. Notes on African Onitini mainly from Southeastern Kenya. *Zoologische Mededelingen Leyden* 51: 141–170.

Krikken, J. 2009. Drepanocerine dung beetles: a group overview, with description of new taxa. *Haroldius* 4: 3–30.

Kryger, U., Deschodt, C., Davis, A.L. & Scholtz, C.H. 2006. Effects of cattle treatment with a cypermethrin/cymiazol spray on survival and reproduction of the dung beetle species *Euoniticellus intermedius* (Coleoptera: Scarabaeidae). *Bulletin of Entomological Research* 96: 597–603.

Kryger, U., Deschodt, C., Davis, A.L. & Scholtz, C.H. 2007. Effects of cattle treatment with a fluazuron pour-on on survival and reproduction of the dung beetle species *Onthophagus gazella (Fabricius). Veterinary Parasitology* 143: 380–384.

Lacordaire, J.T. 1856. Histoire naturelle des insectes. Genera des Coléoptères ou exposé méthodique et critique de tous les genres proposés jusqu'ici dans cet ordre d'insectes. Tome troisième contenant les familles des pectinicornes et lamellicornes. Librairie Encyclopédique de Roret, Paris: 1–594.

Lansberge, J.W. van. 1874a. Observations sur la classification des Lamellicornes coprophages. *Annales de la Société Entomologique de Belgique* 17: 177–193.

Lansberge, J.W. van. 1874b. Description de quelques Lamellicornes Coprophages. *Coleopterologische Hefte* 12: 4–12.

Lansberge, J.W. van. 1875a. Observations sur la classification des Lamellicornes coprophages. *Annales de la Société Entomologique de Belgique* 17: 177–193.

Lansberge, J.W. van. 1875b. Monographie des Onitides. *Annales de la Société Entomologique de Belgique* 18: 1–148.

Lansberge, J.W. van. 1882. Enumeration des Scarabaeides rapportés du pays des Somalis (Afrique Equatoriale) par M. Révoil. Avec diagnoses des espèces nouvelles. *Annales de la Société Entomologique de Belgique* 26: 21–31.

Lansberge, J.W. van. 1883. Description de trois espèces nouvelles d'*Onthophagus* appartenant au Musée Royal de Leyde. Note VII. *Notes from the Leyden Museum* 5 :14–16.

Lansberge, J.W. van. 1885a. Note III. Description de quatre espèces nouvelles de Coprophages appartenant au Musée de Leyde. *Notes from the Leyden Museum* 7: 17–20.

Lansberge, J.W. van 1885b. Descriptions d'espèces nouvelles de Coléoptères appartenant au Musée civique de Gênes. *Annali del Museo Civico di Storia Naturale Giacomo Doria* 2: 375–400.

Lansberge, J.W. van. 1886. Scarabaéides, Buprestides et Cerambycides de l'Afrique occidentale, envoyés au Musée de Leyde par MM. Veth et Van der Kellen (Note XIII). *Notes from the Leyden Museum, Leyden* 8: 69–120.

Lansberge, J.W. van. 1887. Note III. Cinq espèces nouvelles de Coléoptères exotiques appartenant au Musée de Leyde. *Notes from the Leyden Museum, Leyden* 9: 107–112.

Latreille, P.A. 1802. Histoire Naturelle, Générale et Particulière des Crustacés et des Insectes. Tome troisième. F. Dufart, Paris: 464.

Latreille, P.A. 1804. Histoire naturelle, générale et particuliere des crustacés et des insectes. Paris 10: 1–445.

Latreille, P.A. 1807. Genera Crustaceorum et Insectorum secundum Ordinem naturalem in Familias disposita, Iconibus Exemplisque plurimis explicata (1806-1809). A. Koenig Parisis et Argentorati Volume I–IV 2: 1–280.

Latreille, P.A. 1810. Considérations générales sur l'ordre naturel des animaux composant les classes des crustacés, des arachnides, et des insectes; avec un tableau méthodique de leurs genres, disposés en familles. F. Schoell, Paris: 444.

Latreille. P,A. 1823. Description des Insectes d'Afrique receuillis par M. Cailliaud Voyage à Méroé. Debure, Paris 4: 279–287.

Latreille, P.A. 1825. Familles Naturelles du Règne Animal, Exposées Succinctement et Dans un Ordre Analytique avec l'indication de Leurs Genres. Encyclopédie Méthodique. J.-B. Baillière, Paris: 1–570.

Latreille, P.A. 1829. Le Règne Animal Distribué d'Après son Organisation, pour Servir de Base a` l'Histoire Naturelle des Animaux et d'Introduction à l'Anatomie Comparée. Par M. Le Baron Cuvier, avec Figures Dessinées d'Après Nature. Nouvelle Édition, Revue et Augmentée. Tome IV. Crustacés, Arachnides et Partie des Insectes. Déterville, Paris, France.

Leach, W.E. 1815. Entomology. In: *Edinburgh Encyclopaedia*, volume 9, part 1; Brewster (ed.); Edinburgh: 57–172.

LeConte, J.L. 1861. Article III. Classification of the Coleoptera of North America, part 1. *Smithsonian Miscellaneous Collections, Washington* 3: 1–286.

Le Peletier, A.L.M. & Serville, J.G.A. 1828. Scarabé, *Scarabaeus.* In: *Encyclopédie Méthodique*. Histoire Naturelle. Entomologie, ou Histoire Naturelle des Crustacés, des Arachnides et des Insectes, volume 10, part 2; Latreille, P.A., Le Peletier, A.L.M., Serville, J.G.A., Guérin-Méneville, F.E. (eds); Mme Veuve Agasse, Paris: 346–382.

Lesne, P. 1900. Collections entomologiques recueillies au cours de la mission Bonchamps et remise au Muséum par M. Ch. Michel. Coléoptères. In: Mission de Bonchamps. Vers Fachoda à la rencontre de la mission Marchand à travers l'Éthiopie. Plon-Nourrit et Cie, Paris: 498–501.

Lewis, G. 1895. On the Lamellicorn Coleoptera of Japan, and notices of others. *Annals and Magazine of Natural History* (*series 6*) 16: 374–408.

Linnaeus, C. 1758. Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis, edition 10, volume 1. Laurentii Salvii, Stockholm.

Löbl, I. 2006. New nomenclatural and taxonomic acts, and comments: Scarabaeidae: Scarabaeinae. In: *Catalogue of Palaearctic Coleoptera*. Volume 3: Scarabaeoidea – Scirtoidea – Dascilloidea – Buprestoidea – Byrrhoidea; Löbl I, Smetana A. (eds.); Apollo Books, Stenstrup: 31–32.

Lumaret, J.-P. & Moretto, P. 1983. Contribution à l'étude des Oniticellini: nidification et morphologie larvaire d'*Oniticellus rhadamistus* (F.) et considerations sur la position taxonomique de cette espèce. *Annales de la Société Entomologique de France* (*N.S.*) 19: 311–316.

Macleay, W.S. 1821. Horae entomologica: or essays on the annulose animals. S.Bagster, London 1: 161–524.
Marchisio, R. & Zunino, M. 2012. Il genere *Copris* Müller Tassonomia, filogenesi e note di zoogeografia. *WBA Monographs* 2, Verona: 1–176.
Masumoto, K. 1987. Coprophagid beetles from Northwest Thailand I. *The Entomological Review of Japan* 42: 125–131
Maud, R.R. 2012. Macroscale geomorphic evolution. In: *Southern African Geomorphology: Recent Trends and New Directions*; Holmes P, Meadows M. (eds); Sun Media, Bloemfontein: 5–21.
McGeoch, M.A., Van Rensburg, B.J. & Botes, A. 2002. The verification and application of bioindicators: a case study of dung beetles in a savanna ecosystem. *Journal of Applied Ecology* 39: 661–672.
Medina, C.A. & Scholtz, C.H. 2005. Systematics of the southern African genus *Epirinus* Reiche: descriptions of new species and phylogeny. *Insect Systematics & Evolution* 36: 1–16.
Mittal, I.C. 2011. Synoptic key to Indian species of genus *Garreta* Janssens with a new species from Haryana (India). *Journal of Entomological Research* 35: 295–298.
Mlambo, S., Sole, C.L. & Scholtz, C.H. 2015. A molecular phylogeny of the African Scarabaeinae (Coleoptera: Scarabaeidae). *Arthropod Systematics & Phylogeny* 73: 303–321.
Moczek, A.P. 2002. Allometric plasticity in a polyphenic beetle. *Ecological Entomology* 27: 58–67.
Monaghan, M.T., Inward, D.J.G., Hunt, T. & Vogler, A.P. 2007. A molecular phylogenetic analysis of the Scarabaeinae (dung beetles). *Molecular Phylogenetics and Evolution* 45: 674–692.
Montreuil, O. 1998. Analyse Phylogénétique et Paraphylie des Coprini et Dichotomiini. Scénario Biogéographique. *Annales de la Société Entomologique de France* (*N.S.*) 34: 135–148.
Montreuil, O. 2014. Deux nouveaux *Sisyphus* Latreille de Tanzanie. *Bulletin de la Société Entomologique de France* 119: 177–180.
Montreuil, O. 2015a. Le genre *Neosisyphus* Müller en Afrique. *Catharsius, La Revue* 12: 1–36.
Montreuil, O. 2015b. Nouveaux *Sisyphus* Latreille d'Afrique *Bulletin de la Société Entomologique de France* 120: 91–102.
Montreuil, O. 2015c. Premiers cas de brachyptérisme dans le genre *Sisyphus* Latreille. *Annales de la Société Entomologique de France* (*N.S.*) 51: 281–293.
Montreuil, O. 2017. Nouveaux *Sisyphus* Latreille, 1807, du groupe *seminulum* : le complexe *arboreus*. *Bulletin de la Société Entomologique de France* 121: 167–174.
Moretto, P. 1998. *Kheper festivus* (Harold): un complexe d'espèces. *Entomologia Africana* 3: 27–38.
Moretto, P. 2004. Description de nouveaux *Proagoderus* d'Afrique et remarques sur quelqeus espèces peu ou mal connues (2ème contribution à la révision des *Proagoderus*). *Entomologia Africana* 9: 20–47.
Moretto, P. 2007. Les *Onitis* Fabricius, 1798 du XIIIème groupe de Janssens, espèces nouvelles et espèces affines. *Entomologia Africana* 12: 2–14.
Moretto, P. 2008. *Catharsius karlwerneri*, nouvelle espèce d'Afrique de l'Est. Révision des Catharsius Hope, 1837 du groupe "*heros*". *Entomologia Africana* 13: 38–44.
Moretto, P. 2009. Essai de classification des *Onthophagus* Latreille, 1802 africains des 5ème et 6ème groupes de d'Orbigny. *Nouvelle Revue d'Entomologie* (*N.S.*) 25: 145–178.
Moretto, P. 2010. Les Scarabéides coprophages de Bayanga en République Centrafricaine. *Bulletin de la Société Entomologique de France* 115: 455–477.
Moretto, P. 2011. Nouveaux Scarabaeidae africains appartenant aux genres *Lophodonitis* Janssens, 1938 et *Copris* Müller, 1764. Notes sur quelques *Onitis* Fabricius, 1798. *Catharsius, La Revue* 3: 9–19.
Moretto, P. 2013a. Descriptions de nouveaux *Onthophagus* Latreille, 1802 d'Afrique tropicale. Notes de taxonomie et de faunistique. *Entomologia Africana* 18: 48–55.
Moretto, P. 2013b. La validité du nom du niveau genre *Proagoderus*. Descriptions de deux nouveaux *Proagoderus* Lansberge, 1883, d'Afrique tropicale, et de la femelle de *Proagoderus cerathoterium* Janssens, 1953. *CATHARSIUS La Revue* 8: 1–11.
Moretto, P. 2016a. Description d'un nouveau Canthonini de Namibie appartenant au genre *Dicranocara* Frolov & Scholtz, 2003 (Coleoptera, Scarabaeidae). *Entomologia Africana* 21: 47–49.
Moretto, P. 2016b. Description d'une nouvelle espèce de *Scarabaeolus* Balthasar, 1965, d'Afrique de l'Ouest (Coleoptera, Scarabaeidae). *CATHARSIUS La Revue* 13: 8–23.
Moretto, P. & Nicolas, J.L. 2002. Description de cinq nouveaux *Proagoderus* d'Afrique. *Entomologia Africana* 7: 29–37.
Moretto, P. & Nicolas, J.L. 2004. Emmendata: un nouveau nom pour *Proagoderus palestrinii* Moretto & Nicolas, 2002. *Entomologia Africana* 9: 48.
Moretto, P. & Perissinotto, R. 2013. Description and ecology of two new species of *Gyronotus* van Lansberge, 1874 from southern Africa. *ZooKeys* 344: 73–82.
Mostert, L.E. & Holm, E. 1982. Notes on the flightless Scarabaeina with a description of a new species. *Cimbebasia* A 5: 273–284.
Motschulsky, V. 1860. Sur les Collections Coléoptèrologiques de Linné et de Fabricius. (Continuation). XXII. Lamellicornes. *Études Entomologiques*, 8: 147–162.
Mucina, L. & Rutherford, M.C. 2006. The vegetation of South Africa, Lesotho and Swaziland. *Strelitzia* 19: 1–807.
Müller, G. 1942. Nuovi coleotteri dell'Africa Orientale (2a serie). *Atti del Museo Civico di Storia Naturale di Trieste* 15: 63–86.
Müller, G. 1947. Nuovi Coleotteri dell'Africa orientale (Quarta serie). *Atti del Museo Civico di Storia Naturale di Trieste* 16: 81–93.
Müller, G. 1949. Nuovi coleotteri dell'Africa orientale: V serie. *Atti del Museo Civico di Storia Naturale di Trieste* 17: 152–161.
Mulsant, É. 1842. Histoire naturelle des Coléoptères de France. Lamellicornes. [Tome 2]. Maison Libraire, Paris: 623.
Nguyen-Phung, T. 1987. Révision des *Copris* afro-tropicaux V. Une nouvelle espèce du <groupe fidius Olivier>. [Col. Scarabaeidae]. *Bulletin de la Société Entomologique de France* 91: 271–273.
Nguyen-Phung, T. 1988a. Révision des espèces Afrotropicales du genre *Copris*. IV. Le groupe *fidius* Müller, 1764 [Coleoptera, Scarabaeidae]. *Revue française d'Entomologie, Paris* (*N.S.*) 10: 5–15.
Nguyen-Phung, T. 1988b. Révision des espèces afro-tropicales du genre *Copris* Müller, 1764 VI. Le groupe *bootes* Klug (Coleoptera, Scarabaeidae). *Nouvelle Revue d'Entomologie* (*N.S.*) 5: 247–258.
Nguyen-Phung, T. 1988c. Révision des espèces afrotropicales du genre *Copris* Müller, 1764, VII. Le groupe *corniger* Sahlberg. [Col. Scarabaeidae]. *Bulletin de la Société Entomologique de France* 92: 209–219.

Nguyen-Phung, T. 1989. Révision des espèces afrotropicales du genre *Copris* Müller, 1764 (Coleoptera: Scarabaeidae). VIII. Le groupe *orion* Klug. *Annales de la Société Entomologique de France* (*N.S.*) 25: 199–208.

Nguyen-Phung, T. & Cambefort, Y. 1986a. Révision des espèces afro-tropicales du genre *Copris* Müller, 1764. I. Le groupe *integer* Reiche (Coleoptera, Scarabaeidae). *Nouvelle Revue d'Entomologie* (*N.S.*) 3: 401–416.

Nguyen-Phung, T. & Cambefort, Y. 1986b. Révision des espèces afro-tropicales du genre *Copris* Müller, 1764. III. Le groupe *inhalatus* Quedenfeldt [Coleoptera, Scarabaeidae]. *Revue française d'Entomologie, Paris* (*N.S.*) 8: 100–106.

Nguyen-Phung, T. & Cambefort, Y. 1987. Révision des espèces afro-tropicales du genre *Copris* Müller, 1764. II. Le groupe *jacchus* (Fabricius) (Coleoptera Scarabaeidae *s. str.*). *Annales de la Société Entomologique de France* (*N.S.*) 23: 67–75.

Ochi T., Kon M. & Bai M. 2009. Three new species of *Copris* from China, with description of a new subgenus. *The Entomological Review of Japan* 64: 207–216.

Ochi, T., Kon, M. & Masumoto, K. 2012. A new species of the genus *Parascatonomus* from the Malay Peninsula. *Kogane, Tokyo* 13: 139–142.

Olivier, A.G. 1789. Entomologie, ou histoire naturelle des insectes, avec leurs caractères génériques et spécifiques, leur description, leur synonymie, et leur figure enluminée. Coléoptères. Baudouin, Paris 1: 1–190.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., d'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. & Kassem, K.R. 2001. Terrestrial ecoregions of the world: a new map of life on Earth. *Bioscience* 51: 933–938.

Orbigny, H. d'. 1900. Supplement au synopsis des Onthophagides paléarctique. *L'Abeille* 29: 289–300.

Orbigny, H. d'. 1902. Mémoire sur les Onthophagides d'Afrique. *Annales de la Société Entomologique de France* 71: 1–324.

Orbigny, H. d'. 1904. Onthophagides africains de la collection du Musée Civique de Gênes. *Annali del Museo Civico di Storia Naturale "Giacomo Doria", Genova* 41: 253–331.

Orbigny, H. d'. 1905. Onthophagides provenant du voyage de M. Alluaud dans l'Afrique orientale et descriptions d'autres espèces africains nouvelles. *Annales de la Société Entomologique de France* 74: 381–536.

Orbigny, H. d'. 1908. Descriptions d'espèces nouvelles d'Onthophagides africains et notes synonimiques. *Annales de la Société Entomologique de France* 77: 65–208.

Orbigny, H. d'. 1910. Collections receuillis par M. Maurice de Rothschild en Abyssinie et dans l'Afrique orientale anglaise. Coléoptères: Onthophages. *Bulletin du Musée Nationale d'Histoire Naturelle, Paris* 16: 308–310.

Orbigny, H. d'. 1913. Synopsis des Onthophagides d'Afrique. *Annales de la Société Entomologique de France* 82: 1–742.

Orbigny, H. d'. 1915. Synopsis d'un genre nouveau d'Oniticellides special a Madagascar. *Annales de la Société Entomologique de France, Paris* 84: 402–434.

Palestrini, C. 1982. Il "sottogenere" *Pseudonthophagus* Balth. (Coleoptera : Scarabaeidae : Onthophagini). *Bollettino della Società Entomologica Italiana* 114: 97–102.

Palestrini, C. 1992. Systematica é zoogeografica del genere *Onthophagus* sottogenere *Proagoderus* Lansberge. *Memoirie della Società Entomologica Italiana, Genova* 71: 1–358.

Palestrini, C. & Giacone P. 1988. Filogenesi e zoogeografia del sottogenere *Hyalonthophagus* nov. Atti XV Congresso Nazionale Italiano di Entomologia L'Aquila: 319–327.

Palestrini, C. & Giacone, P. 1989. Systematics Phylogeny and biogeography of the subgenus *Hyalonthophagus*. *Elytron* 3: 79–101.

Pallas, P.S. 1781. Icones Insectorum praesertim Rossiae Sibericaeque pecularium quae collegit et Descriptionibus illustravit. Walther, Erlangae: 1–96.

Partridge, T.C. & Maud, R.R. 1987. Geomorphic evolution of southern Africa since the Mesozoic. *South African Journal of Geology* 90: 179–208.

Paschalidis, K.M. 1974a. The genus *Sisyphus* Latr. (Coleoptera: Scarabaeidae) in Southern Africa. MSc. Thesis, Rhodes University, Grahamstown, South Africa, pp 183.

Paschalidis, K.M. 1974b. The identity of two species in the genus *Sisyphus* (Coleoptera: Scarabaeidae). *Journal of the Entomological Society of Southern Africa* 37: 299–303.

Paulian, R. 1932. Description d'un nouveau genre et d'une nouvelle espèce de coprophage du Tonkin. *Bulletin de la Societe Entomologique de France, Paris* 37: 205–206.

Paulian, R. 1933. Révision des Coptodactylini. *Bulletin de la Société Entomologique de France, Paris* 38: 67–74.

Paulian, R. 1937. Sur quelques nouveaux onthophagides africains et australiens. *Arbeiten uber morphologische und taxonomische Entomologie aus Berlin-Dahlem, Berlin-Dahlem* 4: 336–346.

Paulian, R. 1939. Trois nouveaux coprophages de Mauritanie. *Revue Française d'Entomologie* 6: 10–16.

Paulian, R. 1945. III Coléoptères Scarabéides de l'Indochine. Première partie. Faune de l'Empire Français. Librairie Larose, Paris: 225.

Paulian, R. 1953. Recherches sur les insectes d'importance biologique à Madagascar. XX. Les Scarabaeini de Madagascar. *Mémoires de l'Institut scientifique de Madagascar (E)* 3: 24–27.

Paulian, R. 1975. Sur quelques Canthonina montagnards de Madagascar. *Annales de la Société Entomologique de France, Paris* (*N.S.*) 11: 221–252.

Paulian, R. 1986. Quelques modifications dans la nomenclature des coléoptères Scarabéides. *Nouvelle Revue d'Entomologie* (*N.S.*) 3: 214.

Paulian, R., Cambefort, Y. & Mauchamp, B. 1982. Deux nouveaux Pedaria. *Bulletin de la Société Entomologique de France, Paris* 87: 13–15.

Pereira, F.S. 1954. O género *Scatonomus* Er. (Coleoptera, Scarabaeidae). *Revista Brasileira de Biologia* 1: 53–78.

Pereira, F.S. & d'Andretta, M.A.V. 1955. Novos escarabeidos e novas sinonimias (Col. Scarabaeidae). *Papéis Avulsos do Departamento de Zoologia, Secretaria da Agricultura, S. Paulo, Brasil* 12: 247–264.

Péringuey, L. 1885. First contribution to the South-African Coleopterous Fauna. *Transactions of the South African Philosophical Society* 3: 74–149.

Péringuey, L. 1888. Second contribution to the South-African Coleopterous Fauna. *Transactions of the South African Philosophical Society* 4: 67–194.

Péringuey, L. 1892. Third contribution to the South-African Coleopterous Fauna. *Transactions of the South African Philosophical Society* 6: 1–94.

Péringuey, L. 1896. Descriptions of new genera and species of Coleoptera from South Africa, chiefly from Zambezia. *Transactions of the Entomological Society of London* 2: 149–189.

Péringuey, L. 1901. Descriptive catalogue of the Coleoptera of South Africa. *Transactions of the South African Philosophical Society* 12: 1–563.

Péringuey, L. 1908. Descriptive catalogue of the Coleoptera of South Africa. Additions and corrections. *Transactions of the South African Philosophical Society, Cape Town (1907)* 13: 547–752.

Perty, J.A.M. 1830. Insecta Brasiliensia. In: Spix J, Martius C: Delectus animalium articulatorum, quae in itinere per Brasiliam annis MDCCCXVII-MDCCCXX jussu et auspiciis Maximilliani Josephi I. Bavariae regis augustissimi peracto. Frid. Fleischer, Monachii [München]: 1–60.

Philips, T.K. 2016. Phylogeny of the Oniticellini and Onthophagini dung beetles from morphological evidence. *ZooKeys* 579: 9–57.

Philips, T.K. & Bell, K. 2008. *Attavicinus*, a new generic name for the myrmecophilous dung beetle *Liatongus monstrosus*. *The Coleopterists Bulletin* 62: 67–81.

Philips, T.K. & Scholtz, C.H. 2000. A new genus and species of trichome-bearing dung beetle from South Africa. *African Entomology* 8: 227–231.

Pokorný, S. & Zídek, J. 2009. Review of the Gymnopleurini. I. Introduction and the genus *Allogymnopleurus*. *Folia Heyrovskiana Series A* 17: 133–149.

Pokorný, S. & Zídek, J. 2015. Checklist of *Kheper* Janssens and description of a new species from northern Tanzania. *Insecta Mundi* 0429: 1–7.

Pokorný, S., & Zídek, J. 2018. Review of the Gymnopleurini (Coleoptera: Scarabaeidae: Scarabaeinae). IV. African species of *Garreta* Janssens, with description of a new species from Guinea. *Folia Heyrovskiana Series A* 26: 105–109.

Pokorný, S., Zídek, J. & Werner, K. 2009. Giant dung beetles of the genus *Heliocopris*. Taita Publishers, Czech Republic: 1–135.

Preudhomme de Borre, A. 1880. Note sur le genre *Macroderes* Westwood. *Annales de la Societe Entomologique de Belgique* 23: 7–11.

Quedenfeldt, G. 1884. Verzeichniss der von Herrn Major a D von Mechow in Angola und am Quango-strom 1878–1881 gesammelten Pectinicornen und Lamellicornen. *Berliner entomologische Zeitschrift* 28: 265–340.

Raffray, A. 1877. Coléoptères Lamellicornes rapportés par M.A. Raffray d'Abyssinie et Zanzibar. Descriptions des espèces nouvelles. *Revue et Magazine de Zoologie, Paris* 5: 312–336.

Reiche, L.J. 1841. Tableau d'une division systématique de la tribu des Coprophages dans la famille des Lamellicornes. *Revue Zoologique* 4: 211–213.

Reiche, L. 1848. Ferret A. & Galinier: Voyage en Abyssinie dans les provinces du Tigre, du Samen et de l'Amhara (1839-1843). Tome I–III (1847–1848). Entomologie. Paris (1849) 3: 304–361.

Reitter, E. 1893. Bestimmungstabelle der Lucaniden und coprophagen Lamellicornen. XXIV. Heft, (Sonderabdruck aus dem XXX. Bande der Verhandlungen des naturforscheden Vereins in Brünn). Verlag des Verfassers, Brünn: 3–230.

Ritsema, C. 1888. Lijst der entomologische Geschriften van Mr. J.W. van Lansberge, gevolgd door eenen opgawe der daarin beschreven nieuwe geslachten, ondergeslachten en soorten. *Tijdschrift voor Entomologie* 31: 201–234.

Roets, F. & Oberlander, K.C. 2010. *Silvaphilus*: a new relict forest-endemic Canthonini dung beetle genus from the Western Cape Province of South Africa. *African Entomology* 18: 369–373.

Roets, F., Crous, C. & Pryke J. 2017. *Sarophorus diabolus* sp. n. and *Sarophorus frolovi* sp. n. (Coleoptera: Scarabaeidae: Scarabaeinae) from South Africa. *African Entomology* 25: 264–270.

Roggero, A., Barbero, E. & Palestrini, C. 2015. Phylogenetic and biogeographical review of the Drepanocerina. *Arthropod Systematics & Phylogeny* 73: 153–174.

Roggero, A., Barbero, E. & Palestrini, C. 2016. Revised classification and phylogeny of an Afrotropical species group based on molecular and morphological data, with the description of a new genus. *Organisms Diversity & Evolution* DOI 10.1007/s13127-016-0297-z: 1–18.

Roggero, A., Dierkens, M., Barbero, E. & Palestrini, C. 2016. Combined phylogenetic analysis of two new Afrotropical genera of Onthophagini. *Zoological Journal of the Linnean Society* doi: 10.1111/zoj.12498: 1–23.

Roggero, A., Moretto, P., Palestrini, C. & Barbero, E. 2019. The phylogenetic relationships of *Tiaronthophagus* n.gen. (Coleoptera, Scarabaeidae, Onthophagini) evaluated by phenotypic characters. *Insects* 10: 3390.

Rossi, P. 1792. Mantissa Insectorum, exhibens species nuper in Etruria collectas, adiactis Faunae Etruscae illustrationibus, ac amendationibus (1792–1794). Typographia Polloni. *Pisis* 1: 1–154.

Roth, J.R. 1851. Diagnosen neuer Coleoptera aus Abyssinien. *Archiv für Naturgeschichte, Berlin* 17: 115–133.

Rougon, D. & Rougon, C. 1982. Le comportement nidificateur des Coléoptères Scarabaeinae Onilicellini en zone sahélienne. *Bulletin de la Société Entomologique de France* 81: 272–279.

Sahlberg, C.R. 1823. Periculi Entomographici, species Insectorum nondum descriptas propositour. Fasciculus, Insecta Fennica, 1–82.

Schäfer, P. & Fischer, E. 1992. Zur Scarabaeiden-Fauna Rwandas, Zentralafrika. 1. Sisyphini. *Senckenbergiana biologica* 72: 119–137.

Schäfer, P. & Fischer, E. 2001. Zur Scarabaeidenfauna Rwandas, Zentralafrika 2, Gymnopleurini und nachtrag Sisyphini. *Mitteilungen des internationalen entomologischen Vereins supplement* 9: 1–93.

Scheuern, J. 1988. Zur taxonomie der gattung *Liatongus* mit beschreibung einer neuen art aus Bhutan. *Entomologica Basiliensia* 12: 305–317.

Scholtz, C.H. & Howden, H. 1987. A revision of the African Canthonina. *Journal of the Entomological Society of Southern Africa* 50: 75–119.

Scholtz, C.H. & Howden, H. 1987. A revision of the southern African genus *Epirinus*. *Journal of the Entomological Society of Southern Africa* 50: 121–154.

Schoolmeesters, P. 2017. Scarabs: World Scarabaeidae Database (version Jan 2017). In: Species 2000 & ITIS Catalogue of Life, 29th May 2017. Digital resource at www.catalogueoflife.org/col. Species 2000; Roskov Y, Abucay L, Orrell T, Nicolson D, Bailly N, Kirk PM, Bourgoin T, DeWalt RE, Decock W, De Wever A, Nieukerken E van, Zarucchi J, Penev L (eds) (2017); Naturalis, Leiden, the Netherlands. ISSN 2405-8858.

Schreber, J.C.D. 1759. Novae species Insectorum. *Halae, Schneider*: 1–16.

Sharp, D. 1880. Note sur quelques espèces du genre *Macroderes*. *Annales de la Société Entomologique de Belgique* 23: 36–39.

Shibuya, T. & Inouchi, J. 1982. Fine structure and odor responses of olfactory sensillae of the Japanese dung beetle,

Copris pecuarius (Coleoptera: Scarabaeidae). *Japanese Journal of Applied Entomology and Zoology*, 26: 194–195.
Shipp, J.W. 1895a. The coprophagous Lamellicornia: a list of species belonging to the genera *Circellium* and *Sceliages*, with notes on Ateuchidae. *The Entomologist* 28: 37–40.
Shipp, J.W. 1895b. *Gymnopleurus*; correction of nomenclature. *The Entomologist* 28: 2–3.
Shipp, J.W. 1895c. Notes on *Onthophagus* Latr., with corrections of nomenclature, and a description of a new genus. *The Entomologist* 28: 178–179.
Shipp, J.W. 1895d. *Onthophagus*: correction in Nomenclature. *The Entomologist* 28: 221–222.
Shipp, J.W. 1895e. A revised classification of the genus *Ateuchus* Weber. *The Entomologist* 28: 218–221.
Shipp, J.W. 1896a. *Irrorhotides*: a new genus of Ateuchidae, with a description of a new species. *The Entomologist* 29: 116–4117.
Shipp, J.W. 1896b. On a new species of *Ateuchus* (*Actinophorus*) from Australia. *Novitates Zoologica* 3: 72.
Shipp, J.W. 1897a. I. Coleoptera by Dr Karl Jordan. Appendix 1. Scarabaeidae. In: A. Donaldson Smith, *Through unknown African countries: the first expedition from Somaliland to lake Lamu.* E. Arnold: London, New York: 448–452.
Shipp, J.W. 1897b. On the genus *Gymnopleurus*, Illiger; with a list of species and descriptions of two new genera. *The Entomologist* 30: 62–66, 131–135, 166–168.
Silvestri, F. 1924. Description of a new myrmecophilous Scarabaeidae of India. *Records of Indian Museum* 26: 583–586.
Simonis, A. & Zunino, M. 1980. Il genere *Cyptochirus*. *Bollettino del Museo di Zoologia dell'Università di Torino* 4: 21–40.
Smith, A.G. 2006. A review of the family-group names for the superfamily Scarabaeoidea with corrections to nomenclature and a current classification. *Coleopterists Society Monograph* 5: 144–204.
Smith, A.G. 2009. Checklist and nomenclatural authority file of the Scarabaeoidea of the Nearctic realm. Version 4 – released 22 April 2009. Available at http://museum.unl.edu/research/entomology/SSSA/Nearctic-Scarabs4.pdf.
Spector, S. 2006. Scarabaeine dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae): an invertebrate focal taxon for biodiversity research and conservation. *The Coleopterists Bulletin Monograph Number* 5: 71–83.
Steven, C. von 1809. Descriptions de quelques insectes du Caucase et de la Russie méridionale. *Mémoires de la Société Imperiale des Naturalistes de Moscow* 2: 31–42
Strassen, R. zur. 1961a. Eine neue *Scarabaeu*s art aus Südafrika. *Senckenbergiana Biologica* 42: 437–441.
Strassen, R. zur. 1961b. Einige seltene Sudafrikanische *Scarabaeus* arten im Mus. Frey mit einer neu-beschreibung. *Entomologische Arbeiten aus dem Museum G. Frey* 12: 236–241.
Strassen, R. zur. 1962. Beschreibung einiger neuer oder verkannter südafrikanischer *Scarabaeus*-Arten. *Senckenbergiana Biologica* 43: 339–357.
Strassen, R. zur. 1963. *Scarabaeus andreaei*, ein neuer Pillendreher aus Mozambique. *Senckenbergiana Biologica* 44: 107–110.
Strassen, R. zur. 1965. Zur Kenntnis Gattung *Sceliages* Westwood, mit zwei Neubeschreibungen. *Senckenbergiana Biologica* 46: 219–232.
Strassen, R. zur. 1967. Arten ubersicht der gattung *Scarabaeus* Linnaeus mit besonderer berucksichtigung der Athiophischen formen. *Entomologische Blätter für Biologie und Systematik der Käfer* 63: 129–173.
Strassen, R. zur. 1980. A new species of *Scarabaeus* Linnaeus, 1758 from coastal sand areas in Natal. *Journal of the Entomological Society of Southern Africa* 43: 107–112
Tagliaferri, F., Moretto, P. & Tarasov S. 2012. Essai sur la systématique et la phylogénie des *Onthophagus* Latreille, 1802, d'Afrique tropicale appartenant au septième groupe de d'Orbigny. Description d'un sous-genre nouveau et de trois espèces nouvelles. *Catharsius, La Revue* 6: 1–31.
Takano, H. 2018. A systematic revision of the Afrotropical members of the dung beetle genus *Catharsius* Hope, 1837 (Coleoptera: Scarabaeidae). D. Phil. thesis, University of Oxford.
Tarasov, S.I. & Dimitrov, D. 2016. Multigene phylogenetic analysis redefines dung beetles relationships and classification. *BMC Evolutionary Biology* 16: 1–19.
Thomson, C.G. 1859. Skandinaviens Coleoptera. Synoptiskt bearbetade. I. Tom. Berlingska Boktryckeriet, Lund: 290.
Thunberg, C.P. 1818. Coleoptera Capensia antennis lamellatis, sive clava fissili instructa. *Memoires de l'Academie imperiale des Sciences de Saint Petersburg* 6: 395–450.
Tshikae, B.P., Davis, A.L.V. & Scholtz, C.H. 2013a. Dung beetle assemblage structure across the aridity and trophic resource gradient of the Botswana Kalahari: patterns and drivers at regional and local scales. *Journal of Insect Conservation* 17: 623–636.
Tshikae, B.P., Davis, A.L.V. & Scholtz, C.H. 2013b. Does an aridity and trophic resource gradient drive patterns of dung beetle food selection across the Botswana Kalahari? *Ecological Entomology* 38: 83–95.
Tyson, P.D. 1986. *Climatic change and variability in southern Africa*. Oxford University Press, Cape Town.
Vaz de Mello, F.Z. 2008. Synopsis of the new subtribe Scatimina, with descriptions of twelve new genera and review of *Genieridium*, new genus. *Zootaxa* 1955: 3–75.
Vinson, J. 1946. On *Nesosisyphus*, a new genus of coprine beetles from Mauritius. *Proceedings of the Royal Entomological Society of London* 15: 89–96.
Wall, R. & Beynon, S. 2012. Area-wide impact of macrocyclic lactone parasiticides in cattle dung. *Medical and Veterinary Entomology* 26: 1–8.
Wallengren, H.D.J. 1881. Coleoptera Transvaliensia. Bidrag till kännedora où Transvaal-Landets I S. Africa Coleopter-fauna. *Entomologisk Tidskrift, Stockholm* 2: 9–22.
Walter, P.H. 1976. Un nouveau *Metacatharsius* du Zaire et de République Populaire du Congo. *Bulletin de la Société Entomologique de France* 81: 267–270.
Walter, P.H. 1982. Contribution à la connaissance des scarabaeides corprophages du Gabon. I. Trois espèces nouvelles de la région de Makokou. *Revue francaise d'Entomologie, Paris* (*N.S.*) 4: 167–171.
Walter, P.H. 2014. Les *Caccobius* Thomson, 1859, appartenant au couplet 65/12 du 'Synopsis' de d'Orbigny. *CATHARSIUS La Revue* 10: 9–34.
Walter, H. & Lieth, H. 1964. Klimadiagramm-Weltatlas. Jena: Gustav Fischer.
Wasmann, E. 1918. Myrmecophile und termitophile coleopteren aus Ostindien. *Wiener Entomologische Zeitung* 37: 1–23.
Waterhouse, C.O. 1876. On various new genera and species of Coleoptera. *Transactions of the Royal Entomological Society Fourth Series*: 11–25.

Waterhouse, C.O. 1888. On some Coleoptera from eastern Equatorial Africa received from Emin Pasha. *Proceedings of the Zoological Society of London*, 86–87.

Waterhouse, C.O. 1890. XLVII. New Scarabaeidae in the British Museum. *The Annals and Magazine of natural History, including Zoology, Botany and Geology, London* 6: 365–373.

Waterhouse, C.O. 1891. New Scarabaeidae in the British Museum: a fifth contribution. *The Annals and Magazine of natural History, including Zoology, Botany and Geology, London* 6: 507–522.

Weber, F. 1801. Observationes Entomologicae, Continentes Novorum Quae Condidit Generum Characteres, et Nuper Detectarum Specierum Descriptiones. Bibliopolii Academici Novi, Kiel, Germany.

Westwood, J.O. 1837a. Partington C.F. British Cyclopaedia of Natural History: Combining a scientific classification of animals, plants and minerals; with a popular view of their habits, economy, and structure. Orr & Smith London 2: 55.

Westwood, J.O. 1837b. Characters and descriptions of some new coleopterous insects, belonging to the family of sacred beetles. *Proceedings of the Zoological Society of London* 5: 12–13.

Westwood, J.O. 1839. Descriptions of insects figured in plate 9 and 10. Royle J.F.: Illustration of the Botany and other Branches of the Natural History of the Himalayan Mountains and of the Flora of Cashmere. I. London 7: 53–55.

Westwood, J.O. 1842. Descriptions of some new exotic genera belonging to the family of the sacred beetles. *Proceedings of the Royal Entomological Society of London*: 59.

Westwood, J.O. 1844. A memoir containing descriptions of two species of sacred beetles from southern Africa. *Proceedings of the Entomological Society of London (1841)*, 100.

Wiedemann, C.R.W. 1819. Neue Käfer aus Bengalen und Java. *Zoologisches Magazin, Kiel* 1: 157–183.

Wiedemann, C.R.W. 1823. Zweihundert neue Käfer von Java, Bengalen, und dem Vorgebirge der guten Hoffnung. *Akademische Buchhandlung: Kiel Zoologische Magazin* Vol. 2, Part 1: 1–133.

Wiedemann, C.R.W. & Germar, E.F. 1821. Neue exotische Käfer. *Magazin der Entomologie, herausgegeben von Dr. Ernst Germar. J. Chr. Hendel und Sohn, Halle* 4: 107–183.

World Wildlife Fund. 2017. Terrestrial Ecoregions. Available at: https://www.worldwildlife.org/biome-categories/terrestrial-ecoregions.

Ziani, S. & Branco, T. 2011. The authorship and date of the genus-group name *Pachylomera*. *Zootaxa* 2803: 63–68.

Ziani, S. & Gudenzi, I. 2012. Commenti sulla sistematica generica degli Scarabaeini del bacino del Mediterraneo con una chiave dicotomica per il loro riconoscimento (Insecta Coleoptera Scarabaeidae: Scarabaeinae). *Quaderno Di Studi E Notizie Di Storia Naturale Della Romagna* 36: 115–158.

Zídek, J. & Pokorný, S. 2004. Checklist of the genus *Scarabaeus* Linné. *Animma. X* 5: 1–30.

Zídek, J. & Pokorný, S. 2008. Illustrated keys to Palearctic *Scarabaeus* Linné (Scarabaeidae). *Animma. X* 27: 1–27.

Zídek, J. & Pokorný, S. 2011. Replacement name for a subgenus of Scarabaeus Linné, and remarks on *Scarabaeus isidis*. *Klapalekiana* 47: 89–90.

Zídek, J. & Pokorný, S. 2018. New species of the *Scarabaeus* subgenus *Scarabaeolus* Balthasar, with a review of the subgenus (Scarabaeidae: Scarabaeinae: Scarabaeini). *Insecta Mundi* 0611: 1–35.

Zunino, M. 1977. Una nuova specie di *Neopachysoma* della Namibia. *Bollettino del Museo di Zoologia dell'Università di Torino* 2: 15–18.

Zunino, M. 1979. Gruppi artificiali e gruppi naturali negli *Onthophagus*. *Bollettino del Museo di Zoologia dell'Università di Torino* 1: 1–18.

Glossary of scientific terms

The terms cited below are defined only in the context of the present book. Definitions may not be universally applicable. They have been simplified as far as possible for readers who have not received a training in scientific terminology.

5×5 km polygon: The spatial resolution of information (size of squares) on the GIS base maps from which average altitude, temperature and rainfall data were extracted.

A

Abdomen: The hind portion of the beetle body.

Aedeagus: Sclerotised (hardened) reproductive organ of male dung beetles, which may be similar or quite different in shape between species; sometimes aedeagi (plural) are extracted by dissection to confirm the identity of species.

Afrotropical: Major biogeographical region comprising Africa south of the central Sahara Desert; sometimes considered to include Madagascar and southwest Arabia.

Allotype: See 'Type specimens'; a secondary type often created if males and females differ markedly in appearance.

Alluvial soils: Soils deposited in riverine (rivers) or lacustrine (lake) environments.

Alpha taxonomy: The most basic level of taxonomy, i.e. description of animals and plants at species level.

Area of Occurrence (AOO): The area actually occupied by a species (also see 'Extent of Occurrence').

Assemblage: Refers to a co-occurring group of species; species assemblage structure differs geographically, between habitats and between dung types.

Asymmetrical: An irregular pattern.

***Auctorum*:** 'of authors'; conveys that a species name is used in the sense of subsequent authors, which differs to that intended by the original author.

Australasia: Major biogeographical region comprising Australia, New Zealand, New Guinea and nearby islands.

Avermectins: A group of pesticides used to control pests of domestic livestock; they are derived as fermentation products from actinomycete bacteria.

B

Ball roller: One of four major behavioural groups in scarabaeine dung beetles; species that construct and roll balls of dung (also see 'Endocoprid', 'Kleptocoprid', 'Tunneller').

Basal dichotomies: Lower and older levels of branching on an evolutionary tree.

Basally derived: Lineages derived from nodes at the base of an evolutionary tree (also see 'Basal dichotomies').

Bioassay: Use of dung beetles to determine the relative non-target toxicity of different pesticides used on domestic livestock; assessment based on percentage mortality or percentage reduction in breeding success due to pesticide residues in dung.

Biological indicators: Differences in the occurrences of dung beetle species are widely used to indicate effects of changes in vegetation cover (habitat fragmentation) and effects of different pesticides in agricultural landscapes (bioassay).

Biomass: The ecological impact of species varies according to their different body sizes; therefore, assemblages of organisms may be compared by weight, which is termed biomass.

Biome: Largest of three geographical scales used to define floral distribution patterns in South Africa by Mucina and Rutherford (2006) (also see 'Bioregion' and 'Vegetation unit').

Bioregion: Intermediate geographical scale out of three used to define floral distribution patterns in South Africa by Mucina and Rutherford (2006) (also see 'Biome' and 'Vegetation unit').

Bootstrap: Statistical method for defining the strength of a predicted relationship between lineages diverging from a node on an evolutionary tree; usually expressed as a percentage likelihood.

C

Caffraria: An old and inexact term considered to represent southeast southern Africa in its narrowest sense up to the whole of southern Africa in its widest sense; frequently used as an inexact type locality for species described in the earlier part of the 19th century.

Carnivore: In reference to mammals: meat-eating species dropping small amounts of dung that contain high levels of nitrogenous compounds; little known on its relative attraction to dung beetles.

Clade: A branch on an evolutionary tree; may comprise one or more evolutionary lineages.

Cladistic: Evolutionary analysis; subdivision into clades (see 'Clade').

Classification: A hierarchical system that classifies the Class Insecta (insects) into orders, suborders, superfamilies, families, subfamilies, tribes, subtribes, genera, subgenera, species, subspecies, down to varieties.

Clay: The finest-grained division in the United States Department of Agriculture (USDA) classification of soil types (see 'Soil classification').

Cline: A range of variation within a species that matches a geographical gradient, e.g. exoskeleton colour change across a gradient from warmer to cooler temperatures.

Coleoptera: The taxonomic Order to which beetles belong.

Collecting intensity: The relative effort expended on collecting insects, which frequently varies from region to region; such variation may introduce bias into recorded distribution patterns and needs to be recognised.

Collection artefact: Used in explanation when the distribution of a species is poorly known and is suspected to represent under-collection rather than a true pattern of rarity or restricted occurrence related to some environmental factor.

Conspecifics: Individuals occurring in the same species.

Convergence: See 'Morphological convergence'.

Correlation: See 'Correlated'.

Correlated: A relationship between different factors, e.g. between annual rainfall and the occurrence of a species.

Cover density: The degree by which vegetation covers the soil surface or by which the tree canopy shades the soil surface; usually expressed as a percentage.

Critically Endangered (CR): One of the Red List categories of threat designated by the IUCN; used to identify

a species that is considered to face threats that are only one level above Extinction (EX) in the wild (see IUCN categories in Introduction).

D

Data: General term used to refer to any information whether descriptive or quantitative.

Data Deficient (DD): One of the Red List categories of threat designated by the IUCN; used to identify a species for which information is insufficient to assess whether or not it faces any threats of extinction in the wild.

Dentition: Tooth-like projections on the exoskeleton of insects that is often used in taxonomy and classification.

Diel periodicity: Daily period of activity; either walking in flightless species or flying in winged species; may be diurnal (daytime) or active in darkness (nocturnal: night time; crepuscular: dusk and dawn, dusk only, or, rarely, dawn only).

Digital databasing: Computerised listing of information from labels attached to museum specimens is now widespread and forms a large part of the field of study termed: Bioinformatics.

Disjunct: A geographical distribution characterised by gaps between Areas of Occurrence (AOO).

Diurnal: Activity during the hours of daylight.

Diversity: An often loosely used term referring to the scale of differences within a region or an assemblage of organisms (high or low diversity – in numerical terms = large numbers or low numbers).

E

Ecological associations: General term used to refer to associations with the environment at large (e.g. biogeography) or small scales (e.g. habitat, food).

Ecological Impact Assessments (EIA): Studies designed to determine the potential effects of development; for instance if development would be ecologically detrimental or if an area earmarked for development contains threatened species.

Ecoregions: Geographical regions defined by Olson et al. (2001) from patterns of plant and animal distribution. Used here only for areas outside the borders of South Africa.

Ectoparasites: External parasites of animals.

Elytra: The sclerotised (hardened) and modified fore wings of beetles that cover the functional hind wings when they are folded over the dorsal surface of the abdomen; may be fused together in flightless species.

Endangered (EN): One of the Red List categories of threat designated by the IUCN; used to identify a species that is considered to face serious threats of extinction in the wild (see IUCN categories in Introduction).

Endemic: Found only within a specified region or situation and nowhere else.

Endocoprid: One of four major behavioural groups in scarabaeine dung beetles; species that breed within or immediately below droppings in situ (also see 'Ball roller', 'Kleptocoprid', 'Tunneller').

Endoparasites: Internal parasites of animals.

Exoskeleton: The often hard outer layer of the insect body.

Extant: Existing at the present time, i.e. not extinct.

Extent of Occurrence (EOO): The area enclosed by outlining distribution records for a species; if species occupancy is continuous, it will be equivalent to Area of Occurrence (AOO); if species occupancy is disjunct or non-continuous, EOO will be larger than AOO.

F

Family: See 'Classification'.

Flight periodicity: See 'Diel periodicity'.

Fossorial: Associated with the soil.

Frons: From above: the middle part of the head between the clypeus at the front, the vertex at the back and the genae at the sides.

Fungi: Classified at Kingdom level along with plants and animals; includes single up to multicellular organisms; some dung beetles show specialist associations with mushrooms and toadstools on which they feed and breed.

G

Generalisation: See 'Generalist'.

Generalist: A species that shows a wide range of ecological associations without being specialised to any particular factor e.g. found on a range of soil types from sand to sandy loam to clay with no specialisation to any particular one (see 'Specialist').

Genus: Singular of genera; a level of classification of plants and animals (see 'Classification').

GIS base maps: Digital Geographical Information System base maps divided into small squares (polygons) from which computer information may be extracted; in this instance maps for annual rainfall, annual temperature, altitude.

Gradsect: A study comprising data obtained from points along a geographical gradient.

Grain size profiles: The proportional composition of a soil in terms of three different grain sizes (see 'Soil classification').

H

Habitat: Characteristics of an area where an animal is found, e.g. sandy desert, forest, grassland.

Habitat fragmentation: The process of subdivision of natural habitat, primarily through urbanisation, agricultural or industrial development.

Habitat heterogeneity: The relative diversity of habitats in a geographical area.

Habitat transformation: The modification of natural habitat, e.g. conversion of highland grassland to commercial tree plantation in South Africa.

Holotype: See 'Type specimens'; A single type specimen designated to represent the name allotted to a species; may be supported by additional designated types with the status of allotype or paratypes.

Hydrological: Pertaining to water in soils.

Hyrax middens: The toilet areas (middens) used by the rock hyrax, which contain a mass of dung pellets.

I

Improved pasture: Agricultural term referring to the improvement of pasture so that it is more suitable for farming domestic livestock, particularly cattle; natural grassland is often 'improved' through replacement by Kikuyu grass pasture.

***Incertae sedis*:** 'of uncertain placement'. Used in this book when genera have been placed in a tribe, but probably do not belong there.

Indument: A natural covering; in the context used here, material covering the lateral edges of the elytra.

Ingestables: In reference to pesticides administered to domestic livestock orally; toxic pesticide residues are subsequently found in dung.

Injectables: In reference to pesticides administered to domestic livestock by injection; toxic pesticide residues are subsequently found in dung.

Intraspecific: Variation within a species.

Iridescent: Often shiny metallic colouration shown by many dung beetles, which is generated by reflectance of different wavelenths of light from layers in the exoskeleton; different thicknesses of the reflective layers are responsible for the different perceived blue, green or cupreous colours.

IUCN Red List Categories: Categories to describe the relative threat or lack of threat to survival of species designated by the International Union for Conservation of Nature (IUCN).

K

Kleptocoprid: One of four major behavioural groups in scarabaeine dung beetles; species that 'steal' dung buried by other dung beetle species for breeding purposes (also see 'Ball roller', 'Endocoprid', 'Tunneller').

L

Later-derived: See 'Terminally derived'.

Least Concern (LC): One of the Red List categories of threat designated by the IUCN; used to identify a species that is considered to face no threats of extinction in the wild.

Lectotype: See 'Type specimens'; a single specimen selected from a type series containing only syntypes; thereafter, essentially has the status of a holotype.

Lineage: Refers to a single evolutionary line or collection of branched lines originating from a single point in a phylogeny.

Localised: Refers to a small Area of Occurrence (AOO = actual presence) within a large Extent of Occurrence (EOO = the overall range).

Localisation: see 'Localised'.

M

Macrohabitat: Large scale spatial associations, e.g. forest or desert.

Major females: In some dung beetle species, females also show secondary sexual armature that varies in prominence with body size so that it is greater in larger-bodied individuals than in smaller-bodied individuals; however, one rarely sees the terms major or minor females (see 'Sexual dimorphism').

Major males: In many dung beetle species, the prominence of secondary sexual armature is greater in larger-bodied individuals (termed major males) than in smaller-bodied individuals (termed minor males) (see 'Sexual dimorphism', 'Secondary sexual armature').

Means: Essentially average values, but termed means because they are cited together with a standard deviation (SD); SDs merely represent a statistical range within which most data values occurred; the SD also conveys whether there was little variation in data values (small plus or minus deviation in value away from the mean) or a great deal of variation (large deviation in value away from the mean).

Mesic: A relative term for moister as opposed to drier or arid conditions.

Microhabitat: Small scale spatial associations; e.g. in leaf litter, under stones.

Milbemycins: A group of pesticides used to control pests of domestic livestock that are chemically similar to avermectins; they are derived as fermentation products from *Streptomyces* bacteria.

Minimum spanning trees: Method used to statistically link species data points in the NMDS ordinations; these links are depicted by a network of lines joining data points for species that showed the most similar distribution patterns to one another in southern Africa.

Minor females: (see 'Major females').

Minor males: (see 'Major males').

Molecular phylogeny: Evolutionary tree based on analyses of similarity between molecular level characterisation; usually genetic material found in animal or plant cells (DNA sequences).

Monogastric herbivores: In reference to mammals: grazing or browsing herbivores in which there is a single stomach; dung usually coarse-fibred, e.g. elephants, horses.

Monophyletic: Refers to a taxon derived from a single ancestor; monophyletic ancestry may be supported by occurrence on a single evolutionary lineage.

Monotypic: A genus which is represented by a single species.

Morphological phylogeny: Evolutionary tree based on analyses of similarity between characteristics of body shape and body features.

Morphology: Relating to the shape and sculpturing of insect exoskeletons; morphological variation is used to classify insects (see 'Classification').

Morphological: See 'Morphology'.

Morphological convergence: Sometimes seen in distantly related species in separate geographical areas that have independently evolved similar body shape due to similar habits.

Multilayer interference: See 'Iridescent'.

Mycetophage, Mycetophagous: Feeding on fungi.

N

Nearctic: Major biogeographical region comprising North America southwards into higher altititude areas of Mexico.

Near Threatened (NT): One of the Red List categories of threat designated by the IUCN; used to identify a species that is considered to be close to facing threats of extinction in the wild (see IUCN categories in Introduction).

Neotropical: Major biogeographical region comprising South America northwards through central America into lowland parts of Mexico.

Neotype: See 'Type specimens'; a single specimen designated to represent a species name when no previously designated type can be located, often through loss or destruction.

Nest architecture: Immature dung beetles develop within modelled portions of dung, termed broods, that are constructed by the parent(s), mostly within nests in the soil;

the manner of dung burial, brood and nest construction varies between taxa; it can be simple or complex; the characteristics of a nest may be described as nest architecture.

NMDS ordination: Non-metric Multidimensional Scaling ordination: a statistical method used, here, to summarise average similarities or dissimilarities between the geographical distributions of species in southern Africa (represented by data points in a two-dimensional box); the distance between data points provides a rough indication of how close or distant the distribution patterns are for each species or tribe.

Node: In relation to evolutionary trees, refers to the point of branching between lineages.

Nomenclature: Refers to the names used in the classification system.

***Nom. nov.*:** At species level, a new name to replace one that represents duplication of the same name for a species in the same genus described at an earlier date.

O

Olfaction: The sense of smell by which dung beetles locate dung; the olfactory sensory cells are found on the antennae (feelers).

Omnivores: In reference to mammals: a mixed animal and plant diet; omnivore dung is often found to attract more species and individuals than other dung types.

Order: See 'Classification'.

Oriental: Major biogeographical region comprising the more tropical southern regions of southeast Asia, including most of Indonesia.

P

Palaearctic: Major biogeographical region comprising Europe, Northern Asia, North Africa and the Middle East.

Paratype: See 'Type specimens'; additional designated specimens in a type series; often designed to show the range of variation within a species or to act as alternative types if the holotype is lost or destroyed.

***Pars*:** One part of a type series that contains more than a single species in error.

Phylogenetic: Pertaining to phylogeny.

Phylogeny: Evolutionary tree defining relationships between lineages; in this instance, tribes, genera or species of dung beetles.

Polyphyletic: Refers to a taxon with members that occur in different evolutionary lineages; indicates that the taxon is derived from more than one ancestor; also demonstrates that as constituted, at least some included taxa have been misclassified.

Post-mining chronosequence: In reference to mining of dunes for titanium at Richards Bay; refers to the succession of vegetation (grassland, shrubland, woodland) that is restored in sequence following mining of the dune forest.

Pour-ons: Refers to the administering of pesticides poured onto the exterior of domestic livestock to control pests; toxic pesticide residues are subsequently found in dung.

Prothoracic disc: The visible upper part (= pronotal disc) of the thorax (middle section of a dung beetle between the head and hind part).

Psammophilous: Sand-associated.

Pyrethroids: A group of manufactured pesticides used to control pests of domestic livestock that are chemically similar to pyrethrins produced naturally by the plant genus, *Pyrethrum*; toxic pesticide residues are subsequently found in dung.

Q

Qualitative data: Descriptive data based on observations or on numerical data that are not supported by a standardised method.

Quantitative data: Numerical data derived from a standardised method of collection.

R

Radiant heat: Heat projected directly from the sun.

Range fragmentation: Fragmentation of a species range through piecemeal habitat modification, or, in the case of dung beetles, possibly through range contraction by mammals dropping preferred dung types.

Raw data: Data (usually numerical) that has not been analysed further from that first recorded.

Reference material: Stored museum specimens; information on labels attached to validated reference material are

used to determine species geographical distributions and ecological associations.

Regression trees: A statistical predictive modelling technique that was used to classify the South African flora into Vegetation Units, Bioregions and Biomes (see Mucina & Rutherford 2006).

Revalidation: Raising the status of taxa from synonymy with other names back to fully valid genus or species status.

Revision: Refers to a review of previously described taxa, which may include correction of errors, synonymy or revalidation of names and, possibly, the addition of newly described taxa.

Ruminant herbivores: In reference to mammals; grazing or browsing herbivores in which there is a four-chambered stomach; dung usually fine-fibred, may be dropped as pads or pellets, e.g. cattle, sheep.

S

Sand: The coarsest-grained division in the United States Department of Agriculture's (USDA) classification of soil types (see 'Soil classification').

Sandy clay loam: The penultimate division towards finer-grained soils in the United States Department of Agriculture's (USDA) classification of soil types (see 'Soil classification').

Sandy loam: The penultimate division towards coarser-grained soils in the United States Department of Agriculture's (USDA) classification of soil types (see 'Soil classification').

Scarabaeidae: A family of beetles (Order Coleoptera) comprising 16 subfamilies that have diversified primarily in association with living plants and dead or waste organic matter.

Scarabaeinae: Subfamily of the Scarabaeidae to which the dung beetles featured in this atlas are allotted.

Secondary sexual armature: Variously characterised in different species by horns, projections and/or dentition.

***Sensu*:** 'In the sense of'; used here to denote species that were misidentified by an author and listed in the taxonomic literature under the wrong name.

Sexual dimorphism: Refers to the quite different sculpturing of the exoskeleton shown by males of many dung beetle species compared to females; the most frequent examples are presence or absence of horns or projections on the head or prothoracic disc, also, presence or absence of spines on the legs; these features vary in prominence with body size from, so-called, major to minor features; graphs have shown that the variation describes a sigmoid curve with change from major to minor features over a relatively small range in body size; the characters of major males decline in prominence to minor males, which are close in appearance to minor females, whose characters may increase in prominence with body size to those shown by major females.

Sigmoid curve: An S-shaped curve (see 'Sexual dimorphism').

Silt: A medium-sized soil grain (see 'Soil classification').

Soil classification: Based on the system used by the United States Department of Agriculture (USDA): sand, sandy loam, sandy clay loam, clay; each soil type comprises different proportions of large (sand), medium (silt) or small (clay) grains with a bias to either small or larger grain size; soil grain size profiles are important for tunnelling by dung beetles, some species are associated with particular soil types.

Specialisation: See 'Specialist'.

Specialist: A species that shows a narrow range of ecological associations due to specialisation to one or more particular factors (e.g. found only on deep sands, not in finer-grained soil types, such as sandy loam or clay).

Species: See 'Classification'.

Species accounts: Refers to the sum total of information provided for each species.

Species complex: Refers to a cryptic (hidden) group of species that are very close in appearance to one another.

Species richness: In the sense used here: the number of recorded species.

Spectra of released volatiles: Refers to the range of chemicals released into the air from dung, which are perceived by dung beetles by their sense of smell; only particular chemicals within this range elicit a response, which is used to locate the dropping.

Spp.: Species (plural).

Standard deviation: A statistical range of variation around a mean value (see 'Means').

Subfamily: See 'Classification' and 'Scarabaeinae'.

Subsp.: Subspecies.

Subspecies: See 'Classification'.

Succession: Refers to the replacement of different taxa over time (= turn over), e.g. successive replacement of taxa over time in response to the process of drying after deposition of dung.

Superfamily: See 'Classification'; dung beetles of the Subfamily Scarabaeinae are allotted to the Family Scarabaeidae in the Superfamily Scarabaeoidea.

Survivorship: The proportion of individuals in a population surviving over a defined timescale.

Synonym: In taxonomy; a name or names provided for a species, which had already been previously described under a different name; under the rule of precedence, only the first-described species name is valid.

Syntype: See 'Type specimens'; two or more specimens in a type series for which no single specimen was designated as a holotype, nor subsequently as a lectotype; all individuals in the type series are considered to have equal rank; species described a long time ago are often supported by syntypes.

Systematics: Study of the evolutionary relationships between taxa (see 'Phylogeny').

T

Taxa: Plural of taxon.

Taxon: Term of reference for an organism (or organisms) without specifying the level it occupies in the hierarchy of classification (see 'Classification').

Taxonomy: Allotment of taxa to levels in a classification system (see 'Taxon' and 'Classification').

Temporal associations: Refers to time or period of activity at different scales in dung beetles; these may be predictable in response to daily (diel) or seasonal cycles of light and temperature or they may vary non-cyclically in time according rainfall events or from year-to-year according to the cumulative effect of preceding ecologically important factors.

Terminally derived: Lineage derived from a node on higher branches of an evolutionary tree; in terms of sequence of derivation, represents later evolution along the lineage than those branches derived from more basal nodes along the same lineage (also see 'Basally derived').

Textural: Used here in terms of grain size structure of soils.

***Themeda*-dominated grassland:** Many areas of natural grassland on the Highveld of South Africa may be dominated by the genus, *Themeda*.

Topography: The physical surface relief of a geographical area in terms of hills and mountains etc.

Topology: The pattern of clades and lineages on a evolutionary tree; a ladderised topology is one where each successive node gives rise to the remainder of the evolutionary tree.

Tribal: See 'Tribe'.

Tribe: A level of classification of plants and animals (see 'Classification').

Trophic: Pertaining to food type and feeding.

Tunneller: One of four major behavioural groups in scarabaeine dung beetles; species that construct tunnels from under dung into which dung is buried a piece at a time (also see 'Ball roller', 'Endocoprid', 'Kleptocoprid').

Type localities: A single or several localities of origin defined for type specimens of a species.

Type specimen(s): Designated specimen(s) that represent(s) a species name formally described in a publication. Specimen(s) lodged in a museum or scientific collection where it/they may be viewed by other researchers; see holotype, allotype, lectotype, neotype, syntype, paratype.

V

Validated: Confirmation that the name used for a particular species is valid; species identity has been validated for all non-type material in this atlas, unless stated otherwise in the 'Taxonomy' sections of species accounts.

Validation: See 'Validated'.

Varietal: See 'Variety'.

Variety: Represents specified variation within a species, e.g. colour varieties or exoskeleton sculptural varieties; often used to distinguish variation between populations across a geographical range (see 'Classification').

Vegetation classification: Two systems of vegetation classification are used in the atlas, i.e., the hierarchical three-scale classification of Mucina and Rutherford (2006) for South Africa (see 'Biome', 'Bioregion', 'Vegetation unit') and the ecoregion classification of Olson et al. (2001) for the remainder of southern Africa; for

habitat associations; physical structure of vegetation is classified according to increasing shade from grassland, scrub, shrubland, open woodland, woodland and thickets to forest.

Vegetation unit: Smallest of three geographical scales used to define floral distribution patterns in South Africa by Mucina and Rutherford (2006) (also see 'Biome' and 'Bioregion').

Vulnerable (VU): One of the Red List categories of threat designated by the IUCN; used to identify a species that is considered to face threats of extinction in the wild (see IUCN categories in Introduction).

TAXONOMIC INDEX OF AFRICAN TAXA

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SURICATA

1. Atlas and Red List of the Reptiles of South Africa, Lesotho and Swaziland. 2013. M.F. Bates, W.R. Branch, A.M. Bauer, M. Burger, J. Marais, G.J. Alexander and M.S. de Villiers (eds). ISBN 978-1-919976-84-6.
2. Manual of Freshwater Assessment for South Africa: Dragonfly Biotic Index. 2016. M.J. Samways & J.P. Simaika. ISBN 978-1-928224-05-1.
3. A Bilingual Field Guide to the Frogs of Zululand. 2017. Fortunate M. Phaka, Edward C. Netherlands, Donnavan J.D. Kruger, & Louis H. du Preez. ISBN 978-1-928224-19-8.
4. Manual of Afrotropical Diptera. Volume 1. Introductory chapters and keys to Diptera families. 2017. A.H. Kirk-Spriggs & B.J. Sinclair (eds). ISBN 978-1-928224-11-2.
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Accounts and photographs are provided for over 500 scarabaeine dung beetle species recorded in South Africa, Botswana and Namibia. This amounts to an estimated 80% of the regional fauna with the missing species primarily belonging to a single tribe (Onthophagini) for which validation of names and description of new species is an ongoing task. The accounts for tribes, genera and validated species provide information on taxonomic and conservation status, geographical range and distribution, temporal and climatic range, as well as notes on associations with soil, vegetation and food type (where available). Following the species accounts, we have added a short synthesis of current dung beetle systematics and its shortcomings, analyses of group distribution patterns across southern Africa, and threats to conservation of the dung beetle fauna. In addition, several large tables provide quick reference to range size, distribution pattern and conservation status, as well as climatic and ecological associations of each species (where known).

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